

MODELLING THE EFFECT OF HUMAN-CAUSED MORTALITY ON A LION SUB-POPULATION USING SPREADSHEETS

By

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Declaration:

I, the undersigned, hereby declare that the work contained in this assignment is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

Signature.....

Date.....

ABSTRACT

Free-ranging lions (*Panthera leo*) in the Kgalagadi Transfrontier Park (KTP) have been subject to persecution by farmers following livestock depredation in adjacent grazing areas. In recent years at least one adult female was killed annually from a sub-population of five boundary prides that have home ranges adjoining these livestock grazing areas. While no long-term records of human-caused mortality are available, the impact of current rates of human-caused mortality is uncertain. Female-based, age-structured models were thus used to estimate the long-term viability of the KTP lion sub-population subjected to human-caused mortality under deterministic and stochastic environmental conditions. Population parameters incorporated in the models included age-class specific natural mortality, female fecundity and birth sex ratio. In so doing sustainable threshold rates of persecution were established, so that effective conservation measures can be taken, if required, to ensure the continued survival of boundary prides in the park.

Sensitivity analyses of natural survival rates indicated that adult female survivorship is the most important population parameter with respect to maintaining population viability, compared to younger female age-classes, fecundity or birth sex ratio. Hence adults were also the most sensitive age-class with respect to human-caused mortality, as adult survival repeatedly acts upon individuals with the highest reproductive value. In the deterministic model, with the most optimistic survival parameter values, fecundity and birth sex ratio (female-biased) estimates, the sub-population is only able to sustain an annual persecution of three adult females, before the sub-population exhibits a sustained decline. In the worst-case scenario, where fecundity and sex ratio estimates are at their lower extremes, the maximum sustainable age-class specific persecution rate is zero, for all age-classes. Whilst these hypothetical scenarios are unrealistic, they do highlight the extreme thresholds of potentially sustainable persecution rates. Under the most optimistic scenario using the stochastic model, the highest achievable survival probability of the sub-population, when subjected to a persecution rate of one adult annually, was 78%. Although increased fecundity and birth sex ratio biased towards females may increase the survival probability, these parameters are generally at their mean values in the long-term, and may thus not necessarily prevent a sustained population decline. The models therefore suggest that the current persecution rate of one adult annually (or 4% of the adult sub-population), appears unsustainable in the long-term. To ensure the survival of existing boundary prides and to maintain a viable sub-population, adult lionesses should, as far as possible, be afforded protection from persecution.

OPSOMMING

Vrylewende leeus (*Panthera leo*) in die Kgalagadi Oorgrenspark (KTP) is onderworpe aan vervolging deur boere as gevolg van predasie op vee in aangrensende weidingsgebiede. In onlangse jare is ten minste een volwasse wyfie uit 'n subpopulasie van vyf troppe met loopareas wat aan die weidingsgebiede grens, jaarliks uitgewis. Geen langtermyn rekords van vrektes as gevolg van menslike oorsake is beskikbaar nie, en die impak van vrektes wat deur mense veroorsaak word, is dus onseker. Wyfie-gebaseerde, ouderdomgestruktureerde modelle is daarom gebruik om te voorspel wat die langtermyn lewensvatbaarheid is van die KTP leeu subpopulasie wat onderworpe is aan vrektes deur menslike invloede onder deterministiese en stogastiese omgewingsfaktore. Bevolkingsfaktore wat deur die modelle in ag geneem is, sluit ouderdomsgroep-spesifieke natuurlike vrektes, aanwas van wyfies en geboorte geslagsverhouding in. Sodoende is volhoubare uitwissingstempas bepaal sodat, indien nodig, effektiewe bewaringsmeganismes toegepas kan word om die voortbestaan van troppe in die grensgebiede van die park te verseker.

Sensitiwiteitsanalises van natuurlike oorlewingstempas het aangetoon dat volwasse wyfies se oorlewing die belangrikste bevolkingsfaktor is om die bevolking se lewensvatbaarheid te volhou vergeleke met jonger wyfie ouderdomsgroepe, aanwas of geslagsverhouding by geboorte. Daarom was volwassenes ook die sensitiefste vir vrektes as gevolg van menslike invloede, omdat die oorlewing van volwassenes herhaaldelik inwerk op individue met die hoogste reprodutiewe waarde. In die deterministiese model met die mees optimistiese oorlewing, aanwas en geboorte verhouding (wyfie-gebaseerde) beramings, is die subpopulasie slegs in staat om 'n jaarlikse uitwissing van drie volwasse wyfies te onderhou, voordat die sub-populasie 'n volgehoue afname toon. In die uiterste geval waar aanwas en geslags verhouding skattings op die laagste is, is die maksimum volhoubare ouderdomsklasspesifieke beramings nul vir alle ouderdomsklasse. Terwyl hierdie hipotetiese senario's onrealisties is, onderstreep dit die uiterste vlakke van potensiële volhoubare uitwissingstempas. Onder die mees optimistiese senario – 'n uitwissingstempo van een volwassene jaarliks – met die gebruik van die stogastiese model, was die hoogste haalbare oorlewingswaarskynlikheid van die sub-populasie 78%. Alhoewel 'n toename in aanwas en geboorte geslagsverhouding (met oorhelling na wyfies), 'n toename in oorlewingswaarskynlikheid tot gevolg kan hê, is hierdie faktore oor die algemeen gemiddeld oor die langtermyn en sal dit nie noodwendig 'n volgehoue afname in die populasie verhoed nie. Die modelle dui daarop dat die huidige uitwissingstempo van een volwassene (of 4% van

die volwasse sub-populasie) op 'n jaarlikse grondslag onvolhoubaar is oor die langtermyn. Om die oorlewing van bestaande troppe in die grensgebiede, asook 'n lewensvatbare sub-populasie, te verseker, moet volwasse leeuwyfies so ver as moontlik teen vervolging beskerm word.

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CHAPTER 1: GENERAL INTRODUCTION

1.1 Human-caused mortality in perspective

The lion (*Panthera leo*) once achieved a terrestrial range greater than that of any other non-domesticated land mammal (O'Brien *et al.*, 1987). Today free-ranging lions exist almost exclusively in large conservation areas in Africa and in a remote small population in India (Nowell & Jackson, 1996). This marked reduction in both the number and distribution of lions, and indeed other large carnivores, is largely attributed to increased conflict with human development, mainly in the form of settlers and pastoralists (Stander, 1990; Mills, 1991; Stander, 1993; Nowell & Jackson, 1996). Increasing human activities coupled with increasing population growth are ultimately causing habitat loss and persecution of carnivores such as lion, and hence the decline of wild populations (Myers, 1986; Orford *et al.*, 1988; Quigley & Crawshaw, 1992; Stander, 1997). Other factors that may influence the conservation status of lions in Africa, such as trophy hunting and disease, are currently being investigated (Whitman & Packer, 1997). These threats have contributed to the shrinking of the ranges of most large carnivore species and their confinement to marginal habitats or within conservation areas (Hanks *et al.*, 1981; Myers, 1986). However, even conservation areas do not offer full protection and most large carnivore species, especially lions, are subject to persecution when they leave the safety of wildlife sanctuaries (Van der Meulen, 1977; Mills *et al.*, 1978; Anderson, 1981; Stander 1990).

The lion still occurs in fairly large populations within sub-Saharan Africa, and although it is classified globally as actively threatened by high levels of hunting pressure, is not listed within the IUCN Threatened Species categories (1994) (Nowell & Jackson, 1996). In southern Africa, lions are predominantly restricted to a few confined conservation areas where problems with the management and conservation of the species have been experienced over the past several decades (Stander, 1990). Lions in the Kgalagadi Transfrontier Park (henceforth referred to as KTP), an amalgamated wildlife conservation area straddling southwestern Botswana and the extreme Northern Cape Province of South Africa, have been subject to regular persecution by neighbouring farmers in defence of their livestock herds for several decades (Mills *et al.*, 1978; Castley *et al.*, 2001). Most cases of livestock depredation occur when lions break through the fencing that separates the park from the neighbouring farming areas. In retaliation, livestock owners follow up virtually all such incidents, most with the intention of destroying the lions before they can return to the park. Numerically, adult lionesses and their young comprise the largest proportion (67%) of the population that is shot

after transgressing the park boundaries, followed by sub-adult and adult male lions (16 and 17% respectively) (Funston, 2001). The majority of incidents of livestock depredation, and concomitant lion persecution, occur along the fenced boundaries of the KTP. These boundary areas, located within the southern half of the KTP, are occupied by five resident prides, which experience the highest rates of human-caused mortality within the region. It is estimated that approximately one adult female was destroyed each year between 1997 and 2001 from these five boundary prides (Funston, 2001).

The KTP lion population is a natural, free-ranging population currently estimated at 428–478 adults and sub-adults (Funston, 2001). The population density is markedly low (1.3 lions/100 km², Mills *et al.*, 1978; Castley *et al.*, 2001; Funston, 2001) compared to other areas in Africa, such as the Kruger National Park (Smuts, 1978a) and Serengeti Conservation area (Schaller, 1972; Hanby *et al.*, 1995), and is most comparable with that of Etosha National Park in Namibia (1.6–2.0 lions/100 km², Stander, 1991). The relatively low densities of medium-sized ungulate species (0.38 large animal units/km²) is considered the principal cause for low lion densities in the KTP, resulting in lion prides occupying very large home ranges (1462 ± 388 km², Funston, 2001). With a naturally low density and hence relatively small population size compared to similarly sized conservation areas, KTP lions are potentially susceptible to the threats that typically face small populations. These include demographic and environmental stochasticity, and reduced genetic variation, all of which could eventually lead to social instability or extinction (Caughley & Gunn, 1996).

1.2 Modelling objectives and rationale

To estimate whether these five fenced boundary prides are able to sustain the current human-caused mortality rate, age-structured spreadsheet models were used in this study to test the viability of a simulated population under various environmental and demographic conditions. Thus, a model population representative of the five boundary prides, which were amalgamated to constitute a single ‘sub-population’ of the larger KTP lion population, was investigated.

The following questions regarding the persistence of the modelled sub-population are addressed in this study:

1. How sensitive is the equilibrium of the modelled sub-population with respect to demographic parameters?

2. How sensitive is the equilibrium of the modelled sub-population to differential age-class specific human-caused mortality under different environmental conditions and changes in birth sex ratio and female fecundity?
3. Can a modelled sub-population representing the five fenced-boundary prides in the KTP sustain the current rate of human-caused mortality?

Rather than modelling the prides individually, it was decided to model these as an amalgamated 'sub-population', distinct from the larger KTP population. It is considered that modelling at the larger population level may potentially mask possible negative effects of lion persecution along the park boundaries. This is primarily because the largest proportion of the KTP population is buffered from the park boundaries by the boundary prides, and hence, these 'internal' prides are not exposed to persecution. The amalgamation of the five boundary prides is also an attempt to simplify the modelling procedure.

Further, only females and their life histories were modelled, primarily because (1) adult females represent the most heavily persecuted proportion of the population and are thus considered most susceptible to decline, (2) females maintain fixed pride home ranges while males maintain only temporary tenure of a pride (Schaller, 1972), and (3) females are generally the more crucial components ensuring survival of K-selected species (Sibly & Calow, 1986; Caswell, 1989; Crooks *et al.*, 1997). The importance of adult survivorship for population growth has been reported for numerous models dealing with moderate- to long-lived animal species (Wu & Botkin, 1980; Crouse *et al.*, 1987; Caswell, 1989; Crooks *et al.*, 1997). Adult survival acts upon individuals with the highest reproductive value repeatedly, and hence changes in this demographic rate are likely to affect population growth strongly (Crooks *et al.*, 1997). With the aid of age-structured matrix models it has been shown in other felid species, such as cheetah *Acinonyx jubatus* (Crooks *et al.*, 1997) and Iberian lynx *Lynx pardinus* (Gaona *et al.*, 1998), that adult survival is of primary importance to ensure survival of these species.

The synthesis of available data into a population model, followed by sensitivity analysis, may be used to identify those factors or parameters that most decidedly affect the viability of a population (Caswell, 1978). Previous models investigating lion population dynamics were concerned with the effect of various control strategies that were aimed at deliberately

reducing lion density in localised areas (Starfield *et al.*, 1981a; b; Venter and Hopkins, 1988). These models were used to simulate localised lion culling operations in order to describe the effect of long- and short-term localised culling on the total surrounding population, and to demonstrate the importance of the social status of culled lions. The models suggested that the removal of adult males had the greatest impact on the population, because of the social chaos induced by the absence of territorial males. The importance of adult females for ensuring population viability was not apparent from these models, because of the specific model aims. The direction taken by this current spreadsheet approach is to determine the effect of persecution on females only, which represent the most heavily persecuted segment of the study population. In the context of the social group or pride that lions maintain, the stability and the number of adult females are important components that determine the reproductive potential of such a pride, both in terms of producing and successfully raising cubs (Packer *et al.*, 1988). Numerical reduction of pride females through persecution could thus have negative consequences for the sub-population in the KTP.

Concern regarding the future viability of the lion population in the KTP was previously raised by management following the killing of 13 lions on an adjacent Namibian commercial livestock farm in 1996, which initiated a population census in the same year (Castley *et al.*, 2001). However, the area encompassing the five boundary prides still exhibits a healthy lion sub-population, which appears in most respects to be unaffected by persecution (Funston, 2001). Further, the home ranges occupied by most of these prides also appear not to have altered by any appreciable extent over the last 25 years (Mills *et al.*, 1978; Funston, 2001), suggesting that no individual prides have been completely eradicated during this period. This, however, provides inconclusive evidence that the prides have not sustained heavy persecution.

Given limited management resources to effectively limit lion persecution along park boundaries, and the uncertainty of the impact of such persecution, it is desirable to investigate the thresholds of sustainable persecution. With only limited data of population demographics and parameters, a modelling approach may assist in detecting population trends under a given range of scenarios and to elucidate the factors that may be involved in a potential population decline. In so doing the need for effective conservation measures to ensure the continued survival of boundary prides could be identified. The long-term conservation of the lion in the KTP is important from both an ecological and tourism perspective. The lion fulfils an important biological role as a major predator in large natural ecosystems (Smuts, 1978b;

Bertram, 1979; Ruggiero, 1991; Mills *et al.*, 1995) and is considered an essential component of the KTP ecosystem in this regard (Mills, 1990). It also possesses an aesthetic appeal and financial value to tourism-driven conservation areas (Thresher, 1981), such as the KTP.

1.3 Structure of this document

Chapter 2 provides a brief description of the study area. Chapter 3 constitutes a description of the methods used in the development and implementation of the models, as well as the derivation of parameters, and implementation of persecution scenarios. Results obtained from the models are reported in Chapter 4. These include the sensitivities of the various female age-classes, and the maximum sustainable age-class specific human-caused mortality rates. The document is concluded, in Chapter 5, with a discussion on and interpretation of the results in terms of how human-caused mortality may affect the real sub-population.

CHAPTER 2: STUDY AREA

This chapter is devoted to a description of the physical characteristics of the study area within the KTP, which supports the lion sub-population represented in the models of this study. An overview is also given of the population dynamics of the main ungulate prey base of lions in response to rainfall, which is postulated to be the primary influence on the dynamics of the lion population.

2.1 Location

The southern Kalahari is largely a semi-desert region situated in the border area of Namibia, South Africa and Botswana within the southern African subcontinent. It constitutes the most southwestern part of the greater Kalahari Sand area, a vast sheet of aeolian sand, that stretches from the Orange River (c. 29° S latitude) in South Africa to the Congo Basin (c. 1° N latitude) in The Democratic Republic of Congo (Werger, 1978). The KTP, centred within the southern Kalahari between 24° S and 27° S and between 20° E and 22° E, was proclaimed in May 2000 as the first international, cross-border conservation area in southern Africa (Figure 1). It now incorporates two contiguous parks, the Gemsbok National Park (GNP) in Botswana and the Kalahari Gemsbok National Park (KGNP) in South Africa. The KTP covers a surface area of 37 991 km², with adjacent Wildlife Management Areas (WMAs) in Botswana constituting an additional 40 000 km² of conservation area.

The western, southern, and southeastern boundaries of the KTP are enclosed by a “predator-proof” fence, bordering the livestock farming areas in Namibia, South Africa and Botswana respectively (Figure 1). The fence-line is approximately 340 km in extent, with 380 km of the park being unfenced along the northern and northeastern boundaries. The unfenced areas adjoin WMAs, whereas the fenced areas are directly adjacent livestock farming areas. Although not necessarily designated as such, the WMAs effectively create a buffer zone approximately 40 km wide between the park and communal grazing lands to the east and north in Botswana. The area occupied by the lion sub-population adjoins most of the fenced boundaries of the park, including more specifically the Namibian/South African boundary (KTP), the southwestern Mier/KTP boundary (South Africa), and the southeastern Two Rivers/Khawa boundary (Botswana). The population and socio-biological characteristics of the prides residing in the areas adjoining these boundaries have recently been studied (Funston, 2001).

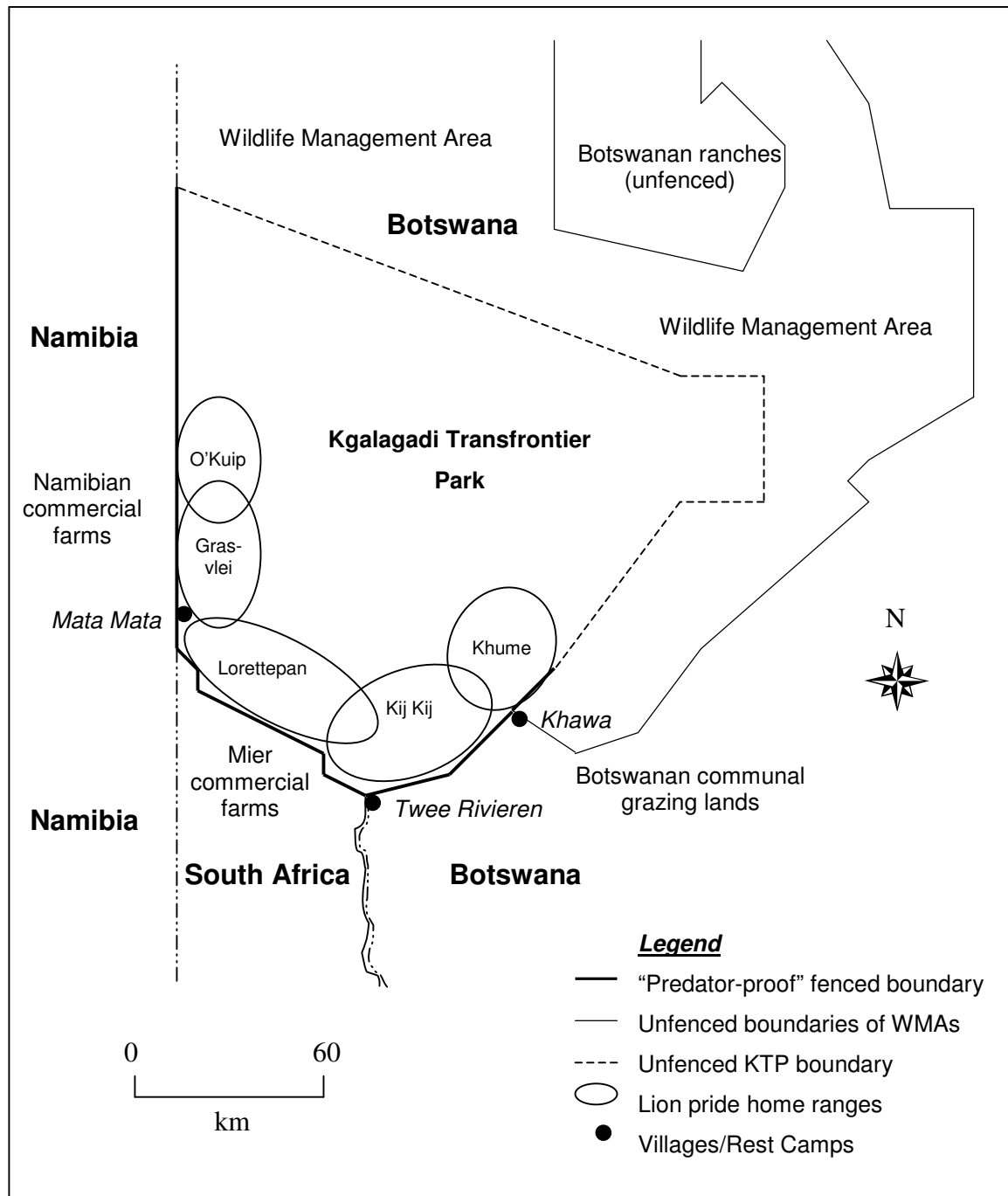


Figure 1. Map showing the approximate home ranges of the five fenced boundary prides in relation to the "predator-proof" fenced and unfenced boundaries of the Kgalagadi Transfrontier Park.

2.2 Geomorphology

The landscape of the park is characterised by extremely low relief and dominated by aeolian sands, at an altitude of about 1000 m (Leistner, 1967). Two ephemeral rivers, the Nossob and Auob, traverse the southwestern part of the KTP in well-developed valleys incised by up to 50 m below the plain in some places. A number of calcrete and salt pans occur interspersed within the KTP and serve as focal points for large herbivores due to their source of minerals

and occasionally water during the wet season (Mills & Retief, 1984). The sand that covers most of the southern Kalahari is thrown into a series of long parallel dunes, which run in a northwest to southeast direction (Leistner, 1967), and are interrupted only by the river valleys and pans. The dunes are typically between 2 to 15 m high with relatively flat tops of up to 9 m wide, and are separated by valleys stretching between 200 and 450 m (Lancaster, 1988). Three varieties of sandy (0.02–2.0 mm diameter), nutrient-poor soils are recognised on the basis of colour, chemical composition and associated vegetation, namely red, pink and white sand (Leistner, 1967). Red sand occurs over the largest part of the southern Kalahari and is the main constituent of the dunes and valleys, with the other sand types restricted to the pans, rivers and dune valleys (Leistner, 1967).

2.3 Climate

The southern Kalahari is roughly located between the 200 and 250 mm isohyets and is characterised by low, irregular annual rainfall (Mills and Retief, 1984). The long-term (1972–1989) mean precipitation for the southwestern part of the KTP, which encompasses the study area, is 215 ± 108 mm (mean \pm standard deviation). Rainfall occurs predominantly in the four months from January to April (Leistner, 1967; Van Rooyen *et al.*, 1990), although three seasons are distinguished: the hot-wet season from January to April, the cold-dry season from May to August, and the hot-dry season from September to December (Mills and Retief, 1984). Ambient temperatures fluctuate widely on a daily and seasonal basis, with the mean maximum and minimum temperatures being 37.4°C and 19.5°C in summer (January) and 22.2°C and 1.2°C in winter (July) respectively (Van Rooyen, 1984; Knight, 1995). The region is subject to drought periods; with an average of three, and a minimum of one to two dry years occurring during any ten-year period (Leistner, 1967). The average duration of drought periods is almost two years.

2.4 Vegetation

The southern Kalahari is an arid savanna or semi-arid desert that forms part of the Savanna Biome of the southern African subcontinent (Huntley, 1982; Van Rooyen *et al.*, 1988). Acocks (1988) considered the vegetation a western form of the Kalahari thornveld, which is mostly an open shrub savanna with scattered trees, becoming increasingly more open down the rainfall gradient towards the south-west (Leistner, 1959; Skarpe, 1986). The southern part of the KTP, which includes that area occupied by the five boundary prides, is characterised by long, parallel, vegetated dunes and shrubby grassland known as dunefields (Leistner, 1967; Skarpe, 1986; Bullard *et al.*, 1995). Within the boundaries of the dunefields three major

habitat-types can be distinguished according to soil types, namely, (1) dunes and undulating sandy flats, (2) dry riverbeds and associated valleys, and (3) pans (Werger, 1978). The river valleys have short to tall grasslands with large trees, such as *Acacia erioloba* and *A. haematoxylon*, being dominant. The dunefields are less sparsely populated with smaller *A. erioloba*, *A. haematoxylon* and *Boscia albitrunca* trees, but support tall (0.5 m) perennial grasses such as *Stipagrostis amabilis*, *S. uniplumis*, *S. ciliata*, *Eragrostis lehmanniana*, *Centropodia glauca* (Leistner & Werger, 1973). Pans are generally bare of vegetation, but support perennials along their periphery in a distinctive zonation pattern (Leistner, 1967).

2.5 The influence of rainfall on lion prey population dynamics

Rainfall, with its particular effect on primary production (Seely, 1978; Rutherford, 1980; Deshmukh, 1984), is widely regarded as the most important element that drives African savanna ecosystems (Coe *et al.*, 1976; Sinclair, 1979; East, 1984; Mills & Retief, 1984; Walker *et al.*, 1987). In arid and semi-arid environments, the biomass of large herbivores is positively correlated with rainfall and primary production, with dry season food shortages limiting the herbivore trophic level (Coe *et al.*, 1976; East, 1984). Food supply thus ultimately limits the tertiary trophic level comprising carnivores (Hanby & Bygott, 1979; Hilborn & Sinclair, 1979; East, 1984), either because numbers of prey are low or because they are less easily caught (Schaller, 1972). However, social behaviour can also play an important role in species such as lion (Schaller, 1972; Bertram, 1973; Smuts, 1978a). The biomass of individual carnivore species is most closely correlated with the biomass of their preferred size class of prey (East, 1984), with lion biomass in particular being significantly correlated to large-sized prey biomass during lean years and lean seasons (Schaller, 1972; Dunham, 1992).

Rainfall is an indicator of forage quality and quantity for herbivores (Scholz & Walker, 1993), with ecological conditions dependent on the fluctuations of annual rainfall related to the long-term mean. Knight (1991) found that the population size estimates of two of the larger Kalahari herbivore species, gemsbok (*Oryx gazella*) and blue wildebeest (*Connochaetes taurinus*), correlated with accumulated rainfall over the preceding two to three years respectively. For gemsbok, their population numbers and exponential rate of increase (r_{\max}) peaked with a two-year average summer rainfall 7.5% above the long-term two-year average mean of 220 mm, but were zero or negative when the average accumulated precipitation was less than 25% below the long-term mean. A population increase in gemsbok, due to high rainfall, is primarily attributable to apparent lower adult and overall calf mortality, while a population decrease following low rainfall would result from low conception rates owing to

decreased body condition of adults (Knight, 1991). Gemsbok are primarily sedentary and do not undertake regular long-distance movements (Verlinden, 1998). They are therefore well adapted to a permanent existence in an unpredictable environment, such as the southern Kalahari. The largest proportion of the gemsbok population of the southern and central Kalahari of Botswana occur within or near protected areas, including the KTP, throughout the year (Verlinden, 1998). They appear to have the ability to fulfil their water and nutritional requirements inside conservation areas, while drought periods of short duration seem to have no marked impact on their population numbers or movements (Verlinden & Masogo, 1997; Verlinden, 1998). Hence they display 'resident' movement patterns within fairly stable home ranges (Knight, 1991).

Gemsbok and wildebeest are the principal large ungulate prey species of lions in the southern Kalahari and comprise as much as 70% of their kills along the riverbeds (Mills, 1984; 1990). Of these two species, gemsbok are the most widely distributed and abundant of the ungulates in the KTP (Knight, 1991), and as lions generally tend to prey on the most common medium-sized ungulates (Mills & Shenk, 1992; Scheel, 1993; Funston *et al.*, 1998) these probably comprise the bulk of their ungulate prey. It is therefore assumed that annual fluctuations in the gemsbok population, depending on the amount of accumulated rainfall in the preceding two years relative to the long-term mean, will influence the ecological conditions for lions, and hence annual lion survival rates. This relationship is supported by observations of population fluctuations in KTP lions in response to long-term environmental conditions (Funston, 2001). The lion population reached its highest recorded size during periods of exceptionally high rainfall sustained for a number of consecutive years (Mills *et al.*, 1978; Funston, 2001) and lowest recorded size following an extended drought period (Castley *et al.*, 2001; Funston, 2001). Rainfall may therefore be considered a direct and indirect driver of ecological conditions that influence lion survival probabilities in the southern Kalahari.

CHAPTER 3: MODEL DESCRIPTION AND METHODS

Age-structured simulation models were developed using a micro-computer spreadsheets, to address the questions posed in the Introduction regarding the viability of the modelled sub-population. Both a deterministic and stochastic model was developed in the course of this study. Only female lions were modelled for simplification, while no behavioural or spatial aspects were considered. Demographic parameters required for developing the models were obtained from the literature where these were considered to be representative of the KTP population, and from a recent study, in which the author was involved, that addressed the population's socio-ecology characteristics (Funston, 2001). These parameters included age-specific survival rates, female fecundity, birth sex ratio and pride-adult recruitment, which were modelled in discrete annual time steps under both deterministic and stochastic conditions. Environmental stochasticity was incorporated into the model as ecological conditions that affect lion survival rates, but not fecundity or birth sex ratios, while demographic stochasticity was not considered.

According to the classification of model types (Holling, 1978), the models in this study may be categorised as models with limited supporting data, but where there is a reasonable understanding of the scenario being modelled. A primary shortcoming of the models is the lack of accurate parameter estimates (the supporting data), despite the deliberate omission of details (second-order effects) in order to maintain simplicity. The models are thus speculative in nature, and are more representative of the what-if approach to problem solving. In particular, the complexities of lion socio-biology (Schaller, 1972; Packer, 1986) that are generally incorporated into detailed programme models (Starfield *et al.*, 1981*a*; *b*; Starfield & Bleloch, 1986; Venter & Hopkins, 1988) were avoided in the spreadsheet models of this study.

3.1 Model time step

A time step of one calendar year was regarded as the most appropriate for the model, as lion age-classes naturally fit well into steps of one-year intervals (e.g. young cubs aged 0–1 years, older cubs aged 1–2 years, sub-adults aged 2–3 years, etc.). Moreover, the process of cub birth occurs at random with no significant birth season (Bertram, 1973; Rudnai, 1973) and hence does not appear to suggest any particular suitable model time step. Each column in the spreadsheet model thus represents one year, in which population processes (calculations) are executed sequentially. A one-year time step also allowed for easier subtraction of lions

removed by human-caused mortality, as all real lion losses are monitored on an annual basis by park management. A period of 50 years was selected as a suitable model horizon, allowing sufficient time to detect potential short-term population decline that would be of concern to park management.

3.2 Age structure of sub-population

The level of detail needed to describe a particular population is an important consideration during the early stages of model development (Norton, 1989). Considering the objective of this model was to investigate the effect of human-caused mortality on females, and since adult survivorship of long-lived species is crucial for ensuring population survival (Caswell, 1989), it was necessary to separate females into year-classes, these being small cubs (aged 0–1 years), large cubs (aged 1–2 years), dependent sub-adults (aged 2–3 years), independent sub-adults (aged 3–4 years) and adults (aged 4 years and older). In the model, cubs aged less than one year of age are referred to as age-class 1 (their number is denoted by x_1), large cubs older than one year but less than two years as age-class 2 (x_2), and so on until age-class 5, representing adults aged 4 years and older (x_5). Newborn cubs (x_0) that are added to the sub-population at the end of each year, do not represent a distinctive and physical age-class, as they are added instantaneously before progressing to cubs aged 0–1 at the beginning of the following year. The initial age structuring of the model sub-population was based on recent observations of the five southern boundary prides (Table 1). In the models no differentiation was made between the prides and all individuals were amalgamated according to the specified age-classes. The prides were aggregated for the model sub-population because there is no migration of lionesses between these. Hence there are no complex interactions involving two or more prides with respect to adult females, which might otherwise warrant a separation of the prides in the models.

Table 1. Age-structure of the five KTP fenced boundary prides in the KTP; December 2000 (Funston, 2001). Individuals in all age-specific classes were amalgamated for the model sub-population.

Age-class	KTP boundary prides					Total
	Grasvlei	Kij Kij	Lorettepan	O’Kuip	Khume	
Cubs (0–1 years)	0	0	3	0	0	3
Cubs (1–2 years)	0	3	0	0	0	3
Sub-adults (2–3 years)	0	0	0	1	2	3
Sub-adults (3–4 years)	4	0	0	0	0	4
Adults (≥ 4 years)	3	5	8	3	3	22

3.3 Annual transition of age-classes

At each annual time step, individuals in each age-class were promoted to the next age-class, while allowing for natural deaths in the intervening year. Thus the number of animals in each age-class at the start of a year was calculated as the number of animals in the previous age-class in the previous year, less those that died as a result of natural mortality. Newborn cubs progress to small cubs the following year, small cubs progress to large cubs, large cubs to dependent sub-adults (2–3 years), dependent sub-adults to independent sub-adults (3–4 years), and independent sub-adults to adults (≥ 4 years). Because all adults are combined into a single age-class, the number of adults proceeds as adults with annual mortality deducted. The process of age-class transition is schematically represented in Figure 2, where x_i and s_i represent respectively the number of individuals in and the survival rates of individuals in age-class i . Female fecundity and the female birth sex ratio, which are discussed later in this chapter, are denoted by f and b respectively.

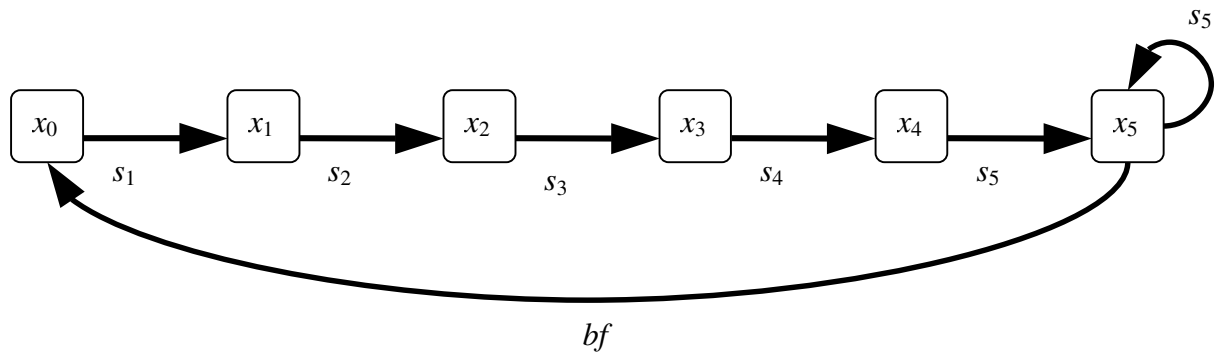


Figure 2. Transition diagram representing the age-class transitions for the model sub-population. Arrows denoted the transitions in the model, from one age-class to another. The number of individuals in and the survival rates of individuals in age-class i is denoted by x_i and s_i respectively. Number of newborn cubs (x_0) produced by the surviving adults, aged four and older (x_5), are added to the population at the end of each model year. Female fecundity is denoted by f , whilst the female birth sex ratio is denoted by b .

3.4 Population processes and model structure

The population processes considered important with respect to the objectives of the model were ordered in a sequence suitable for entering into the spreadsheet (Figure 3), which were then entered into the spreadsheet in a step-wise manner (Appendix A). The models start with the given sub-population age structure, and the subsequent removal and addition of animals executed during a series of mortality (survival and persecution) and reproductive (birth) processes at each time step.

This cycle for each model year begins with the deduction of natural mortality of lions, whereby the number of individuals of each age-class at the end of the previous year are

multiplied by their respective survival rates to obtain the number of individuals at the start of the following year. The formulations used to calculate the number of individuals in each age-class are given in Table 2, these being the same for both the deterministic and stochastic model. The next step allows for the deductions of lions that are persecuted during the intervening year, followed by the calculation of the number of survivors per age-class (lions that survived natural mortality less the number of lions persecuted). The final process calculates the number of offspring produced by adult females that survived until the start of the following year, *i.e.* those adults that remain after both natural and human-caused mortality are deducted.

Table 2. Algorithms used in both the deterministic and stochastic model for calculating the number of individuals in each age-class at the beginning of each year (*i.e.* before human-caused mortality is deducted), except for newborn cubs; these are added to the model sub-population at the end of the year.

Age class	Algorithm
Newborn cubs	$x_0 = bf(x_5 s_5)$
Cubs (0–1 years)	$x_1 = x_0 s_1$
Cubs (1–2 years)	$x_2 = x_1 s_2$
Sub-adults (2–3 years)	$x_3 = x_2 s_3$
Sub-adults (3–4 years)	$x_4 = x_3 s_4$
Adults (≥ 4 years)	$x_5 = x_5 s_5 + x_4 s_5$

The calculations for each of these processes are then repeated over the following year. To avoid decimal values representing lion numbers in the models, all decimal values were converted to the nearest integers, using the rounding function in Excel, *e.g.* where a multiplication results in a product of say 3.4 (number of lions), the value is returned as 3, whilst a product of 3.5 is returned as 4.

3.5 Model assumptions

The models were aimed at addressing the effects of persecution directed at a localised sub-population, and hence a number of assumptions were formulated. A primary assumption stipulated that there was no immigration into the model sub-population from surrounding prides, primarily because recent field observations suggest that prides are unlikely to be entirely eradicated to the extent that immigrating individuals are able to establish themselves in vacant areas, and secondly, it simplifies the model. While emigration of sub-adult females has been reported for the population, no incidents of immigration have been recorded in recent years (Funston, 2001). Lionesses generally reside in subgroups (average of 2.4 adult females; Funston, 2001) of the pride, which are smaller than the average pride size of 4.2

adults, and thus only a portion of the adult pride females are killed should they be persecuted during a boundary transgression. The remaining members of the pride that survive continue to maintain the territory and breed, despite the reduction in pride size. This pattern is assumed during persecution trials in the models, despite individuals of the five prides being amalgamated in the specific age-classes. This assumption is also supported by field observations and management records, where no entire prides have been destroyed during single persecution events to date. This also reduces the possibility of immigration, as the remaining individuals of the prides will not tolerate the presence of immigrating lions (Schaller 1972), preventing the latter from establishing themselves in the sub-population. During a three-year study of the KTP population (Funston, 2001), no immigrating adult females were observed joining existing prides or establishing themselves in the area occupied by the five boundary prides.

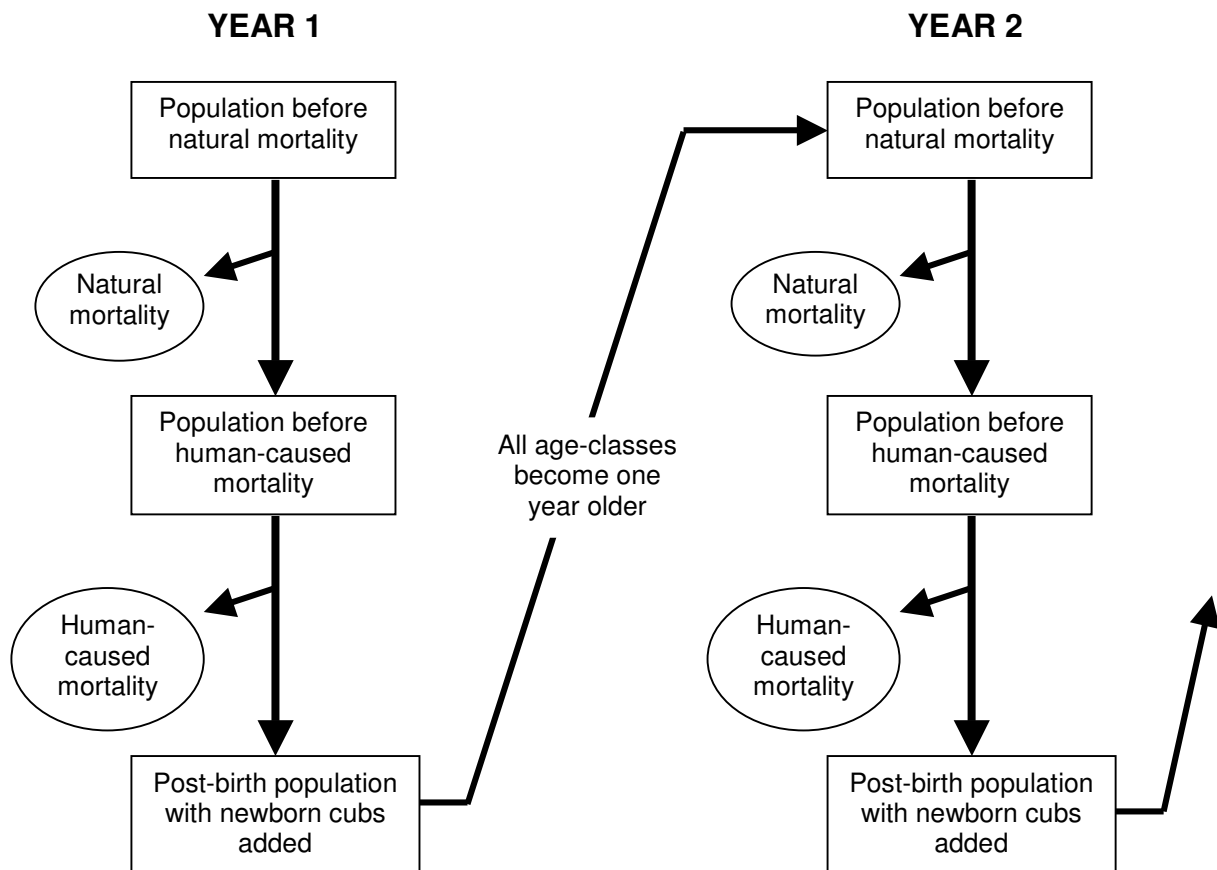


Figure 3. A flow chart depicting the order of population processes in the models. The processes follow a specific order in the spreadsheet to ease calculations. The first process of natural mortality begins at the top left, followed by human-caused mortality, and then the addition of newborn offspring, before all individuals become one year older and pass to the next age-class.

The emigration rate for sub-adult females is low for the KTP population, where only one pride was known to evict a cohort of four sub-adult females; all sub-adults in other prides established themselves in their natal home range (Funston, 2001). In contrast, all sub-adult males were evicted from their natal prides (Funston, 2001). The modelled sub-population of five prides (females only) was therefore considered as an isolated population (as if fenced off from the rest of the population), with population recruitment depending entirely on the reproductive output of the adults in these five prides alone. Emigration was allowed through density-dependent expulsion of independent sub-adults to avoid over-crowding in the sub-population, depending on the number of adult females in the sub-population, as described later in this chapter.

A further assumption was that a minimum of 15 adult females (or three adults per pride) was required to sustain the modelled sub-population, defined as the minimum viable adult population (MVAP). Prides in the KTP consist of an average of 4.2 adult females (Funston, 2001), which is marginally above this minimum. Any further reduction in the number of adults below the MVAP would compromise the reproductive output of the sub-population due to lowered cub survival, as prides constituting three to ten adult females have significantly higher reproductive success in terms of the number of surviving offspring per female, than smaller or larger prides (Packer *et al.*, 1988). Using the MVAP as a potential extinction indicator, rather than complete extinction (*i.e.* zero individuals remaining) would allow park management to respond timely to an inevitable decline, if the causal factors of the decline are not addressed. A final assumption was that age distribution in the deterministic model was stable.

3.6 Model input parameters

The input parameters used in the models were obtained from the literature and from a recent study that addressed the population's socio-ecology characteristics (Funston, 2001). This section that follows is devoted to describing how these parameters were quantified and implemented in the models. The first sub-section is a description of the ecological conditions and environmental stochasticity that ultimately determine lion survival rates, which are dealt with accordingly in the second sub-section. There is, however, no attempt to relate the dynamics of the model sub-population to environmental stochasticity, as this relationship is still poorly understood and cannot be addressed within the scope of this study. The third sub-section describes the process whereby lions are recruited into the adult age-class, followed by the remaining sections dealing with female fecundity and birth sex ratio. The order in which

the parameters are described here thus roughly reflects the order in which they are implemented in the models.

3.6.1 Ecological conditions and environmental stochasticity

In arid and semi-arid environments, dry season food shortages limit the herbivore trophic level, which in turn, limit the tertiary trophic level comprising carnivores such as lion (Coe *et al.*, 1976; Hanby & Bygott, 1979; Hilborn & Sinclair, 1979; East, 1984), as discussed in Chapter 2. The biomass and population dynamics of carnivores is thus influenced primarily by the dynamics of their principal prey species. In the KTP gemsbok constitute the most important and reliable prey species for the lion population, although fluctuations in the number of gemsbok, caused by rainfall, may influence their population dynamics. Thus, in years when the population numbers and exponential rate of increase (r_{\max}) for gemsbok peaks with a two-year average accumulated summer rainfall of 7.5% above the long-term mean (Knight, 1991), it was assumed that the ecological conditions for lions could be considered as *good* owing to improved availability of prey animals. Conversely, when the two-year average accumulated precipitation is less than 25% or more below the long-term mean, resulting in lower numbers of gemsbok, the ecological conditions are assumed to be *poor*. Average accumulated rainfall between these extremes is assumed to generate *average* ecological conditions for lions. It is therefore assumed that annual fluctuations in the gemsbok population influences the ecological conditions for lions, and hence their annual survival rates.

In the deterministic model, three types of environmental scenarios were considered, where each consecutive year for the entire duration of the model was assumed to be poor, average, or good in terms of ecological conditions, thereby representing worst-, average- and best-case scenarios respectively. In the stochastic model, environmental stochasticity was incorporated whereby each year was assigned a random ecological condition, based on a cumulative distribution function. Forty years (1960–2000) of real rainfall data from the KTP was grouped into 11 class intervals (e.g. 50–100, 100–150, 150–200 up to 550–600 mm); the mid-points of each class being the frequency class (class mark). This frequency distribution was then converted to a probability density function (Figure 4). Thus, for each year in the model, a random number between 0 and 1 was generated from a uniform distribution (using the RAND() formula in Excel) to allocate a corresponding annual rainfall value (class mark) from the frequency (probability) distribution (using Excel's VLOOKUP function in conjunction with the probability table as shown in Appendix A). With all years in the model being

allocated a randomly selected rainfall value, the ecological condition of a particular year could then be determined by calculating the average rainfall value for the two preceding years (see formula in cell H1 of Appendix A). The probability of average, poor and good ecological conditions occurring within any 50-year period was determined as 0.50, 0.29, and 0.21 respectively from 1000 replicates of the stochastic simulations (Figure 5). Years with average ecological conditions were thus likely to occur 1.8 times as often as years with poor conditions, and 2.4 times as likely as years with good conditions. A macro in Excel's Visual Basic Editor was used to simulate 1000 iterations of the stochastic model for averaging of the results during sensitivity analysis and persecution scenarios (Appendix B).

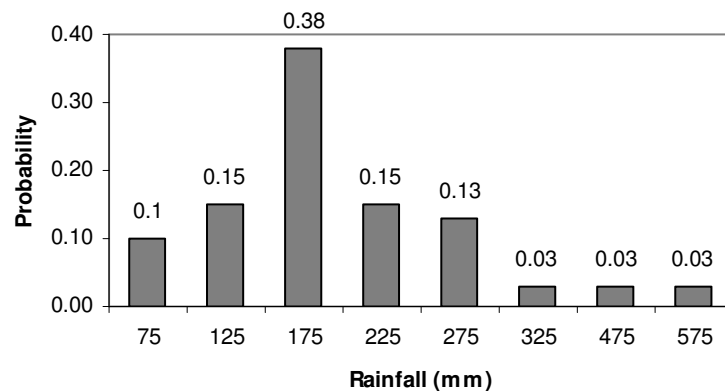


Figure 4. The probability density function for annual rainfall in the KTP, derived from 40 years of real rainfall data.

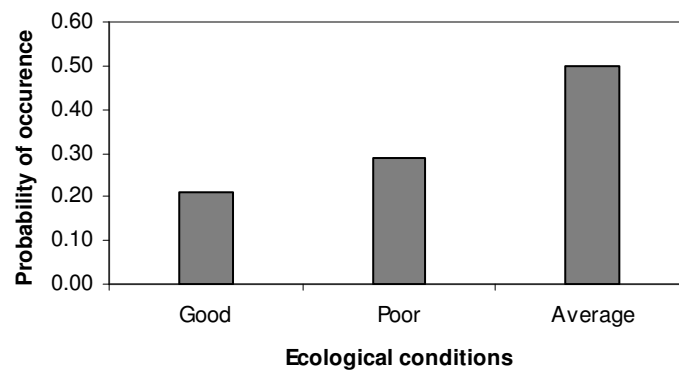


Figure 5. The probability distribution of ecological conditions for any particular year in the model, where a average year, in terms of ecological conditions, is likely to occur 1.8 times as often as a poor year, and 2.4 times as likely as a good year.

3.6.2 Survival rates

No quantitative age-specific survival rates exist for the KTP lion population, while there is a paucity of such data in the literature, and particularly in relation to resource availability or ecological conditions. Best-estimate hypothetical survival rates, based on the ability of an animal to procure sufficient food intake for body maintenance, depending on the age, sex and

social status of the individual, were thus used (Starfield *et al.*, 1981*b*). This ability to obtain food depends on the ecological conditions prevailing during a particular year. Under good ecological conditions lion survival rates are assumed to be higher, particularly for cubs that have better chances of increasing their food intake when principal prey are more abundant. When ecological conditions are poor, lion survival rates are lower (Schaller, 1972; Bertram, 1973; Packer *et al.*, 1988). During such conditions in the KTP, lions would need to hunt smaller mammals more regularly due to scarcity of larger prey (Eloff, 1973; 1984), with the young age-classes of lion subsequently experiencing the effects of food shortage and hence higher mortality (Bertram, 1973). Van Orsdol (1982; *et al.*, 1985) found that cub survival at 12 months was correlated with mean biomass and lean season biomass of prey, indicating that cub survival is dependent on the abundance of food during the period of prey scarcity. Between 12 and 18 months cub survival did not correlate with lean season biomass, indicating lower mortality among cubs older than one year. Cub mortality due to starvation in the Kalahari is apparently high (Eloff, 1980), but largely un-quantified. The level of food availability as a determinant for lion survival rates, which have been used in other, more detailed models (Starfield *et al.*, 1981*a; b*), is not only restricted to prey density, but also other coupled environmental factors that affect hunting success (Van Orsdol, 1982; *et al.*, 1985; Packer *et al.*, 1990; Stander & Albon, 1993; Funston *et al.*, 2001).

A survival rate of 60% has been estimated for cubs until the age of one year (Funston, 2001), over a period of two years that were considered as consecutive average and good ecological conditions. Survival of cubs (0–1 years) in the models was thus given as 60 and 50% during good and average years respectively, increasing to 90 and 75% respectively in the 1–2 year-old age-class. During poor years, cub survival declines to 10 and 30% for first and second year cubs respectively, when starvation reportedly plays a major role in cub mortality (Bertram, 1973; Eloff, 1980; Van Orsdol, 1982; *et al.*, 1985). However, although food availability is a major determinant of cub mortality, and particularly so in seasonal areas (Packer *et al.*, 1988), there are other factors that function in limiting lion populations through cub survival. Other species of predators are known to kill lion cubs (Schaller, 1972; Eloff, 1980) while there is also evidence that cubs die owing to intentional abandonment and accidental maternal neglect (Packer & Pusey, 1984). The relative importance of these causes of cub mortality have, however, not been assessed since the context in which such mortalities occur cannot be defined (Packer *et al.*, 1988). Although infanticide is considered a major cause of cub mortality in most regions (Schaller, 1972; Packer *et al.*, 1988), it is not considered so in the KTP, where no incidents of infanticide were witnessed between 1998 and

2001 (Funston, 2001). Moreover, nearly half of the prides in the KTP are defended by single adult males, with the survival of cubs up to the age of one year not differing significantly from that of prides defended by two or three adult males (Funston, 2001).

Lion survival rates increase with increasing age (Schaller, 1972; Bertram, 1973), with dependent sub-adults having higher survival rates than cubs aged 1–2 years (Table 3). Compared to cubs, adult lions and particularly females have high survival rates (Bertram, 1973; Packer *et al.*, 1988). Orford *et al.* (1988) found an annual mortality rate of 3% for adult lionesses in a similarly arid environment, the Etosha National Park, Namibia, while Rudnai (1973) recorded no adult mortalities in Nairobi National Park over four years. A survival rate of 97% for adult lionesses was thus used for both average and good ecological conditions, similarly as suggested by Starfield *et al.* (1981b). With decreasing ecological conditions all age-specific survival rates decline (Bertram, 1975), with the adult female survival rate declining to 95%.

Table 3. Age-specific survival rates, s_1, \dots, s_5 , of female KTP lions as a function of ecological conditions.

Age-class	Ecological conditions		
	Poor	Average	Good
Cubs (0–1 years)	$s_1 = 0.10$	$s_1 = 0.50$	$s_1 = 0.60$
Cubs (1–2 years)	$s_2 = 0.30$	$s_2 = 0.75$	$s_2 = 0.90$
Sub-adults (2–3 years)	$s_3 = 0.60$	$s_3 = 0.90$	$s_3 = 0.95$
Sub-adults (3–4 years)	$s_4 = 0.85$	$s_4 = 0.95$	$s_4 = 0.97$
Adults (≥ 4 years)	$s_5 = 0.95$	$s_5 = 0.97$	$s_5 = 0.97$

3.6.3 Adult recruitment

Mature sub-adult lionesses are generally recruited into their natal prides, although approximately 30% are expelled from their prides, together with all sub-adult males (Schaller, 1972; Pusey & Packer, 1987; Packer & Pusey, 1993). In some cases an even higher proportion of sub-adult females may remain in their natal prides (Bertram, 1973; Stander, 1991), with approximately 21% of sub-adult females emigrating from their natal prides in the KTP (Funston, 2001). Expulsion of sub-adult females serves to maintain the number of adult females of prides at an optimal level, generally between three and ten individuals, which ensures higher *per capita* reproductive success of the pride (Pusey & Packer, 1987). The size of the natal pride is thus likely to be an important factor determining whether maturing females remain or disperse, as recruitment or expulsion is density dependent (Bertram, 1973; Pusey & Packer, 1987).

Expulsion of sub-adult females was thus incorporated in the models by removing maturing sub-adult females (3–4 years) proportionally as a function of the existing number of adult females in the sub-population. With the average size of KTP prides being 4.2 ± 1.6 adult lionesses (Funston, 2001), the maximum number of adult females allowed in the population of five prides equates to 29 (where each pride contains the maximum number of adult females simultaneously). The total average number of adult females that resided in the five boundary prides between 1998 and 2001 was 24, which was considered as the equilibrium of the sub-population (Funston, 2001) and lower threshold before emigration of sub-adults would manifest itself. The process by which maturing sub-adult females were removed in the model (by reducing their survival rate), was thus defined by the non-linear relationship,

$$s_4 = \begin{cases} s_4^*, & \text{if } 0 \leq x_5 \leq 24 \\ s_4^* (29 - x_5)/5, & \text{if } 24 \leq x_5 \leq 29 \\ 0, & \text{if } x_5 \geq 29 \end{cases}$$

where s_4 represents the variable survival rate of sub-adults (3–4 years), and x_5 the number of adult females (Figure 6). Here s_4^* represents a fixed parameter, being 0.97, 0.95, or 0.85 in

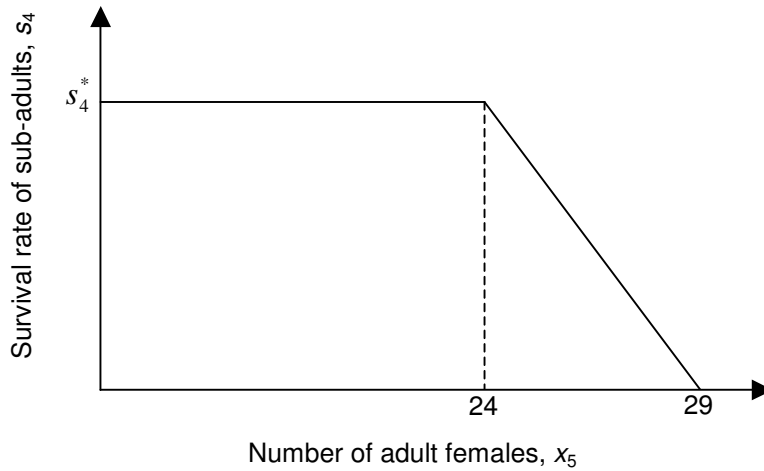


Figure 6. Estimated survival rate of sub-adult females (3–4 years) as a function of the number of adult females in the model sub-population. When the number of adult females is less than 24 individuals, then the survival rate of sub-adults is a fixed parameter, s_4^* , being either 0.97, 0.95, or 0.85 in years with good, average or poor ecological conditions respectively.

years with good, average or poor ecological conditions respectively (see Table 3). When adults number between 24 and 29 the survival rate of sub-adults becomes a variable, s_4 . This procedure was incorporated for each model year and checked the population size at densities when average pride size was exceeded.

3.6.4 Fecundity

The fecundity rate, expressed as births per adult female, was calculated annually from the number of adult females that survived human-caused mortality. An annual fecundity rate of 0.67 cubs/female/year (denoted by f) estimated for KTP lionesses aged four years and older (Funston, 2001), was used in the models. Fecundity was thus expressed as the proportion of adult lionesses that produce one cub every year (67%), which is somewhat lower than that recorded in Etosha National Park (0.87 cubs/female/year, Orford *et al.*, 1988). The fecundity estimate for KTP females includes all lionesses of the known prides and would thus account for the proportion of adults that do not produce cubs, generally between 11 and 15% of the pride adults (Schaller, 1972; Rudnai, 1973). No lionesses younger than four years were observed bearing cubs, which is generally regarded as the minimum reproductive age for lionesses (Rudnai, 1973; Smuts *et al.*, 1978; Orford *et al.*, 1988), hence all adults in the models were assigned as breeding adults. The birth process was executed after the implementation of persecution scenarios, so that newborn cubs (which would be younger than one year) were not orphaned as a direct result of persecution. Although communal suckling is recorded in lions, cubs under the age of one year are susceptible to higher risks of starvation when not supervised by their biological mothers (Pusey & Packer, 1994). Thus for simplicity, persecution was executed before the birth process in the model.

To test the effect of a variable fecundity rate on the viability of the model sub-population subject to human-caused mortality, an upper and lower extreme value of the mean rate was considered. An upper fecundity rate of 0.87 (+30% of mean), which matches the mean rate for lions in Etosha (Orford *et al.*, 1988), was thus considered the most optimistic rate for KTP lions, while a lower bound of 0.47 (−30%) on the mean fecundity rate represents the most pessimistic rate for the model sub-population.

3.6.5 Birth sex ratio

A sex ratio was applied annually to all newborn cubs in order to allocate the desired proportion of female offspring from the newborn cohort to the model sub-population. Although sex ratio at birth does not differ significantly from parity (Bertram, 1973; Smuts, 1976; Smuts *et al.*, 1978; Packer & Pusey, 1987; Creel & Creel, 1997), significantly male-biased (1 : 0.5, 67% male) sex ratios of cubs younger than two years of age have been recorded in the KTP for three consecutive years (Funston, 2001). However, since female-biased cub sex ratios (1M : 1.6F) have been observed before in the KTP (Mills *et al.*, 1978), it is presumed that this population parameter is variable, and that the long-term birth sex ratio

for the KTP is also probably close to parity. Although the ability to produce sex biased litters in accordance with maternal condition (Trivers & Willard, 1973) may be operative among lions, females are able to bias litters when synchronous breeding among pride females is predicted (Packer & Pusey, 1987). The causes of sex-biased litters, however, will not be considered here.

In order to investigate the effect of a variable birth sex ratio on population viability under varying persecution scenarios and ecological conditions, the models were run using both male- and female-biased sex ratios, where the proportion of females (denoted by b) was 0.25 and 0.75 respectively, in addition to an equal ratio ($b = 0.50$). The 50% extremes of the birth sex ratio reflect highly skewed sex ratios, where, for example, one out of a litter of four could differ in sex from the others (Packer & Pusey, 1987). Such biased litters generally occur as a result of social factors operating within individual prides, such as during post-infanticide periods when litters are male-biased more often than by chance (Packer & Pusey, 1987). Although an equal birth sex ratio is expected for lion populations in the long-term, the male-biased sex ratio ($b = 0.25$) serves to investigate the most pessimistic ratio for the sub-population, as this produces fewer potential pride females, and vice versa.

3.7 Model outputs

To evaluate the modelled sub-population's viability subject to persecution, model outputs to monitor population decline were recorded for both the deterministic and stochastic models. The major output for the deterministic model was the maximum sustainable age-specific human-caused mortality rate, P_{\max} , which is that maximum annual rate of individual age-class persecution that is sustainable, and hence does not result in a decline of the model sub-population within a period of fifty years (if there is zero persecution of other age-classes). A persecution rate that did result in the number of adult females reaching less than 15 individuals over a period of 50 years, which represents the minimum viable adult population size (MVAP), was considered unsustainable. For the stochastic model, with 1000 iterations for each persecution trial, the probability (S) that the adult segment of the model sub-population would survive above the MVAP was estimated for each persecution rate (1 to 5 individuals removed annually), as well as the mean time to MVAP for cases when it did not survive, were recorded.

3.8 Sensitivity Analysis

Sensitivity analysis was used to evaluate the effect of each population parameter on selected model outputs individually, in order to identify the key components of the population. This was achieved by changing the parameters by varying amounts to determine the proportional effect on the most important outputs of the model (Norton, 1994). Survival rates were reduced by 1, 5, and 10%, representing respectively a small, moderate and large change. Since survivorship of lions is expected to be fairly sensitive to changes, reduction in survival rates exceeding 10% were not considered. A parameter was considered 'sensitive' if changing that parameter's value by a specified amount lead to a change of the same order or greater in the selected output value (Jackson *et al.*, 2000). Sensitivity analysis was performed for survival rates, female fecundity and birth sex ratio, using both the deterministic and stochastic model.

3.9 Lion persecution scenarios

The effect of human-caused mortality on the model sub-population was estimated with various human-caused mortality trials, or persecution scenarios, whereby the sub-population was subject to various levels of persecution intensity and type. Two main approaches were taken to simulate persecution and its consequences for the model sub-population under both deterministic and stochastic conditions, these being 1) constant, annual persecution of individual age-classes (for the 50 years) and 2) instantaneous but severe reductions in adult lion numbers.

In the first approach and under deterministic conditions, a fixed number of lions, starting from one individual, in each age-class were removed individually (while keeping persecution rates of other age-classes at zero) every year for the entire duration of the model, in order to determine the separating rate that causes a sustained population decline. The smallest persecution rate, k_i , ($i = 1, \dots, 5$) that resulted in such a long-term separation of the population was termed the minimum unsustainable age-specific persecution rate, P_{\min} , and was tested under various combinations of fecundity (with 30% above and below the mean), sex ratio biases (with 50% above and below the mean), and environmental conditions. The maximum sustainable age-specific human-caused mortality rate, P_{\max} , is thus P_{\min} less one individual, and represents the maximum annual rate of individual age-class persecution that is sustainable, and hence does not result in a population decline within a period of fifty years. In the stochastic model the probability (S) of the adult population surviving above the MVAP was estimated for each persecution rate (1 to 5 individuals removed annually) for each age-class, while keeping persecution of other age-classes at zero. The combinations of fecundity

rate and sex ratio biases used in both the deterministic and stochastic model are as follows:

Changes in birth sex ratio only:	Fecundity (0.67) & birth sex ratio (0.25, 0.50, & 0.75)
Changes in fecundity only:	Birth sex ratio (0.50) & fecundity (0.47, 0.67, & 0.87)
Combination of lower extremes:	Birth sex ratio (0.25) & fecundity (0.47)
Combination of upper extremes:	Birth sex ratio (0.75) & fecundity (0.87)

The combination of the lower and upper extreme values of fecundity and birth sex ratio represent the most pessimistic and optimistic scenarios respectively for these parameters. If persecution can be sustained under the most pessimistic scenario, then the real sub-population would be able to sustain similar persecution rates, and possibly higher rates. But if the model sub-population is unable to sustain itself in the most optimistic scenario, then those persecution rates can be considered unsustainable under all circumstances. Prior to implementing persecution scenarios, the deterministic model was run with mean fecundity (0.67) and birth sex ratio (0.50) for the worst-, average-, and best-case scenarios, when ecological conditions were poor, average or good for consecutive years respectively. This was to establish the degree of population viability under the three types of ecological scenarios, without the influence of human-caused mortality. The combinations of fecundity and birth sex ratio were then implemented under each ecological scenario individually and with increasing human-caused mortality. In the stochastic model, where ecological conditions varied annually, the same combinations of fecundity and sex ratios were employed.

Population resilience to individual but severe perturbations was tested by removing 20, 30 and 40% of the adult population at equilibrium instantaneously, using only the deterministic model. Any perturbations larger than 40% would reduce the population to a point below the MVAP within the year the perturbation was introduced, and thus were not considered further. The population was allowed to reach a fixed equilibrium before the persecution perturbation was implemented. Population resilience was measured as the rate (the reciprocal of the return time) at which the population returned to within a band of 37% ($1/e$, where e is the base of the natural logarithm) of its initial displacement from equilibrium (Pimm, 1991). Resilience was thus regarded as zero if the population did not return to within this band after a perturbation from its equilibrium. Although the deterministic model used for testing resilience is non-linear, it may be linearised about the equilibrium state (Jordan & Smith, 1988). Hence for perturbations of the population levels that are not of too great a magnitude from equilibrium, a

linear approximation of the model is valid giving an approximate measure of resilience for the non-linear model.

CHAPTER 4: MODEL RESULTS

The results of the deterministic and stochastic model are presented separately, with respect to both sensitivity analyses and persecution scenarios. Sensitivity analyses were performed by reducing the parameter values by varying amounts to determine the proportional effect on the most important outputs of the models. In the deterministic model the effects of human-caused mortality were determined by removing individuals from each age-class (within a range of 1 to 5 individuals), and noting when a specific rate resulted in an irreversible decline in the adult female segment of the model sub-population. The P_{\max} value is presented as the major model result. The model output in the stochastic model was represented by the survival probability, S , of the model sub-population under the various persecution scenarios.

4.1 Sensitivity analysis

4.1.1 Deterministic model

The sensitivities of the population parameters used in the model were investigated by determining the proportional effect of changes in these parameters on the model outputs. In the deterministic model sensitivity analyses were executed individually under the best- and average-case scenarios, where the sub-population was subjected to successive good and average years respectively, while excluding human-caused mortality. The worst-case scenario (successive poor years) was not considered, since the adult numbers declined irreversibly under the associated conditions (Figure 7). For each parameter change the number of adult females surviving at the end of a 50-year period was recorded, and in cases when the MVAP (< than 15 adults) was reached, the number of years taken to reach the MVAP was also recorded.

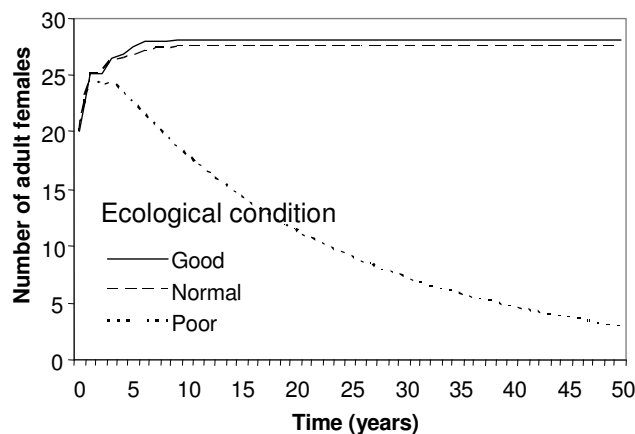


Figure 7. Trend in number of adult females under successive good, average, and poor ecological years. Excluding human-caused mortality, the model sub-population survived only during successive good and average years, representing the best- and average-case scenario respectively.

Under the average-case scenario all age-specific survival rates were insensitive to changes, except that of adults. The annual survival rate of adults was marginally sensitive to a 5% reduction (a survival rate of 0.92) while a 10% reduction (0.87) resulted in the MVAP being reached within 15 years (see Figure 8 or Appendix Table C.1 for a more detailed summary of results). Under the best-case scenario, the adult survival rate was marginally sensitive to a 10% reduction only, while the MVAP was never reached within the simulation period (Figure 9; Appendix Table C.2). Neither fecundity nor birth sex ratio was sensitive to reductions in mean values under the average- (Appendix Table C.3) and best-case scenarios.

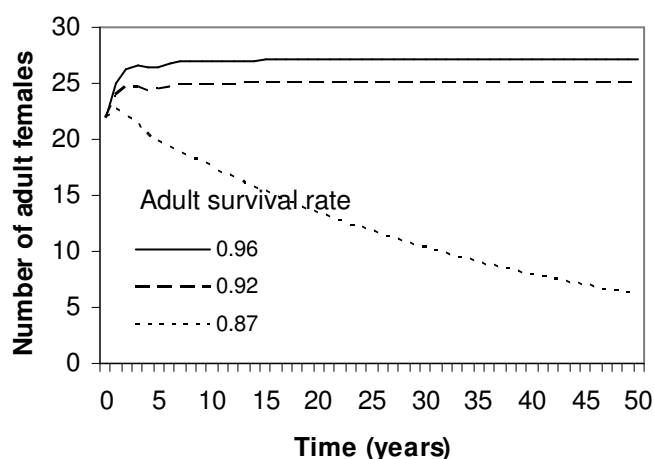


Figure 8. Sensitivity of annual age-specific survival rates in the average-case scenario. The annual adult female survival rate of 0.97 was not sensitive to a 1% (a rate of 0.96) and only marginally sensitive to a 5% reduction (a rate of 0.92), while a 10% reduction (a rate of 0.87) resulted in the MVAP being reached within 15 years.

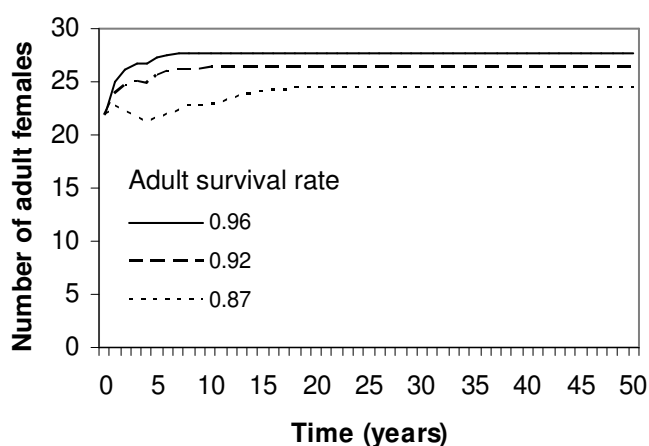


Figure 9. Sensitivity of annual age-specific survival rates in the best-case scenario. The annual adult female survival rate of 0.97 was not sensitive to a 1% (a rate of 0.96) or 5% reduction (a rate of 0.92), but only marginally sensitive to a 10% reduction (a rate of 0.87).

4.1.2 Stochastic model

In the stochastic model, the effect of each parameter change was determined by averaging the results of 1000 simulations subject to environmental stochasticity. The results of each parameter change were summarised as the survival probability (*S*) of the model sub-population, determined as the proportion of times the it survived above the MVAP for the duration of 50 years for each batch of 1000 runs. Also recorded was the mean time (in years) to MVAP for those simulations that resulted in an irreversible decline of the model sub-population. As determined under the deterministic conditions, the annual survival rate of adults was the most sensitive parameter, resulting in 12 and 0% probability of the model sub-population surviving above the MVAP when reduced by 5 and 10% respectively (Table 4). The survival probability was 94% when the adult survival rate was reduced by 1%. The average time to MVAP was 22 and 9 years respectively for a 5 and 10% reduction in the adult survival rate. Younger age-classes were not sensitive to reductions in their survival rates. Further examination of the sensitivity of adult survival (Table 5) demonstrated that a decrease of 2% in the annual rate would reduce the survival probably by more than 20%.

Table 4. Sensitivity analysis of lion survival rates in the stochastic model. The values of the lower, mean and upper survival rates were reduced simultaneously for each parameter change. For each parameter change, the results of 1000 iterations were recorded and summarised as the probability that the model sub-population would survive above its MVAP within 50 years (denoted by *S*). Only adult female survival rates were sensitive, resulting in a survival probability of 94, 12 and 0% when the survival rate was reduced by 1, 5 and 10% respectively. Adult survival was marginally sensitive to a 1% decrease in the annual survival rate.

Age-class	Percent reduction	Resulting change in survival rates			<i>S</i>
		Lower	Mean	Upper	
Cubs (0–1)	– 1%	0.099	0.495	0.594	100%
	– 5%	0.095	0.475	0.570	99%
	– 10%	0.090	0.450	0.540	99%
Cubs (1–2)	– 1%	0.297	0.743	0.891	100%
	– 5%	0.285	0.713	0.855	99%
	– 10%	0.270	0.675	0.810	99%
Sub-adult (2–3)	– 1%	0.594	0.891	0.941	99%
	– 5%	0.570	0.855	0.903	99%
	– 10%	0.540	0.810	0.855	99%
Sub-adult (3–4)	– 1%	0.842	0.941	0.960	99%
	– 5%	0.808	0.903	0.922	99%
	– 10%	0.765	0.855	0.873	99%
Adult (≥4)	– 1%	0.941	0.960	0.960	94%
	– 5%	0.903	0.922	0.922	12%
	– 10%	0.855	0.873	0.873	0%

Table 5. Sensitivity analysis of the adult female survival rate in the stochastic model. The survival probability of the model sub-population was severely compromised where the survival rate was reduced by more than 2%.

Percent reduction	Resulting change in survival rates			S
	Lower	Mean	Upper	
– 1%	0.941	0.960	0.960	95%
– 2%	0.931	0.951	0.951	78%
– 3%	0.922	0.941	0.941	58%
– 4%	0.912	0.931	0.931	30%
– 5%	0.903	0.922	0.922	12%

Similarly as in the deterministic model, sensitivity analysis of fecundity and birth sex ratio indicated that neither of these parameters was sensitive to changes (5, 10, and 20% reduction) in their initial mean values under stochastic conditions (Appendix Table C.4 and C.5).

4.2 Persecution scenarios

4.2.1 Deterministic model

The sensitivity of the trend of the model sub-population within the context of the deterministic model was evaluated separately under two environmental scenarios (average and best-case scenario), with respect to variations in human-caused mortality. The model sub-population was unable to sustain itself when subjected to successive poor years in terms of survival rate estimates (worst-case scenario), even when human-caused mortality was excluded (Figure 7) and irrespective of fecundity or female bias in the birth sex ratio (including a combination of both these parameters at their upper extreme value). Hence, no simulations incorporating human-caused mortality were thus considered under the worst-case scenario.

4.2.1.1 Maximum sustainable persecution rates

Population viability under successive average and good years was tested under various birth sex ratio biases and increasing human-caused mortality (within a range of 1 to 5 individuals annually), with fecundity kept as a constant (0.67). In both the average- and best-case scenarios the sensitivity of the sub-population to human-caused mortality increased with increasing age, while higher persecution rates could be sustained in the best-case scenario (Appendix Table C.6). However, the model sub-population was unable to sustain a persecution rate of one individual per age-class with a male-biased birth sex ratio and mean fecundity ($f = 0.67$) under the average-case scenario. The P_{\max} value increased to one individual under the best-case scenario, and up to three individuals for adult females when the

birth sex ratio became female-biased. Higher rates of persecution could thus be sustained when the sex ratio was either at parity ($b = 0.50$) or female biased ($b = 0.75$) compared to when male-biased ($b = 0.25$).

Similarly to population viability tested under birth sex ratio biases, the sensitivity of the model sub-population to human-caused mortality increased with increasing age-class under variable fecundity rates, while higher persecution rates were sustained in the best-case scenario (Appendix Table C.7). Higher persecution rates were sustained both in the average- and best-case scenarios when fecundity was either at its mean ($f = 0.67$) or upper threshold ($f = 0.87$), compared to when at its lower threshold ($f = 0.47$).

The remaining combinations of fecundity and birth sex ratio were tested, where these were set at their extreme limits (Appendix Table C.8). At a low fecundity rate (0.47) and male-biased sex ratio (0.25), none of the age-classes were able to sustain persecution of any magnitude, irrespective of the best- or average-case scenario. However, with these parameters set at their upper extremes, the model sub-population sustained fairly heavy persecution, although sensitivity to increasing persecution was still evident with increasing age, as expected. The P_{\max} value for adults was two and three adults annually in the average- and best-case scenario respectively (Figure 10).

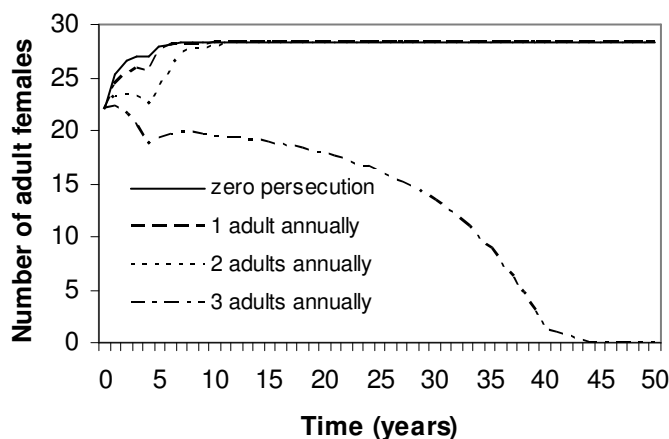


Figure 10. Population viability in the average-case scenario with the most optimistic fecundity and birth sex ratio rates. The maximum sustainable age-specific persecution rate (P_{\max}) under these specific conditions was two adults annually.

4.2.1.2 Population resilience

The effect of single but severe reductions in adult female numbers was determined by measuring the resilience of the model sub-population to increased human-caused mortality among adults. Human-caused mortality was increased individually by removing respectively

20, 30 and 40% of the adult age-class instantaneously at equilibrium, with resilience measured as the rate with which the sub-population returned to within a band of 37% around its initial displacement from equilibrium (Pimm, 1991). As expected, resilience was greater (nearly two-fold) when only 20% of the adults were removed, compared to a 40% reduction. Resilience was also nearly two-fold greater under the best-case scenario compared to the average-case scenario (Appendix Table C.9 and C.10). Resilience was particularly low when fecundity and birth sex ratio were set at their lower extreme rates and especially so in the average-case scenario, where return times of 20 and 47 years respectively were recorded for a 20 and 40% reduction in the number of adult females (Table 6). These return times were markedly reduced under the best-case scenario.

Table 6. Population resilience in the deterministic model to single but severe perturbations directed at the adult female age-class only (instantaneous 20, 30 and 40% reduction from equilibrium), in the best- and average-case scenarios and under combinations of extreme fecundity (f) and birth sex ratio (b) rates. Population resilience was severely retarded in the average-case scenario compared to the best-case scenario, when fecundity and birth sex ratio are at their lower extremes. Cases where the adult population recovered within less than one year, *i.e.* where resilience was very high, are indicated by (-).

	Persecution rate (%)	Best-case scenario		Average-case scenario	
		Return time (years)	Resilience (years ⁻¹)	Return time (years)	Resilience (years ⁻¹)
$f = 0.47$ & $b = 0.25$	20	4	0.25	20	0.05
	30	7	0.14	32	0.03
	40	11	0.09	47	0.02
$f = 0.87$ & $b = 0.75$	20	-	-	-	-
	30	-	-	1	1
	40	-	-	2	0.50

Where large reductions in the number of adults result in long return times to within 37% bands around the original equilibrium, there was no emigration of sub-adult females until the adult population reached the natural equilibrium of 24 individuals. Thereafter, the density-dependent sub-adult expulsion function became operative. Sub-adult females are thus continually recruited into the model sub-population during the recovery period.

4.2.2 Stochastic model

In the stochastic model the viability of the model sub-population was tested by simulating 1000 runs for each persecution scenario (under different levels of fecundity and birth sex ratio) where age-specific human-caused mortality was increased between the range 1 to 5 individuals (while keeping all other age-class human-caused mortality at zero). Sensitivity to persecution increased with increasing age, while survival probability was also low for most

cases where a minimum of only one adult female was persecuted annually, irrespective of the combination of fecundity and birth sex ratio rates (Appendix Table C.11 and C.12).

With the fecundity and birth sex ratio parameters at their mean values, the population was unable to sustain the loss of one adult annually, with only a 15% probability of survival (Figure 11; Appendix Table C.11), and a minimum of 44% when at least one parameter, such as fecundity, was at its upper extreme (Figure 12).

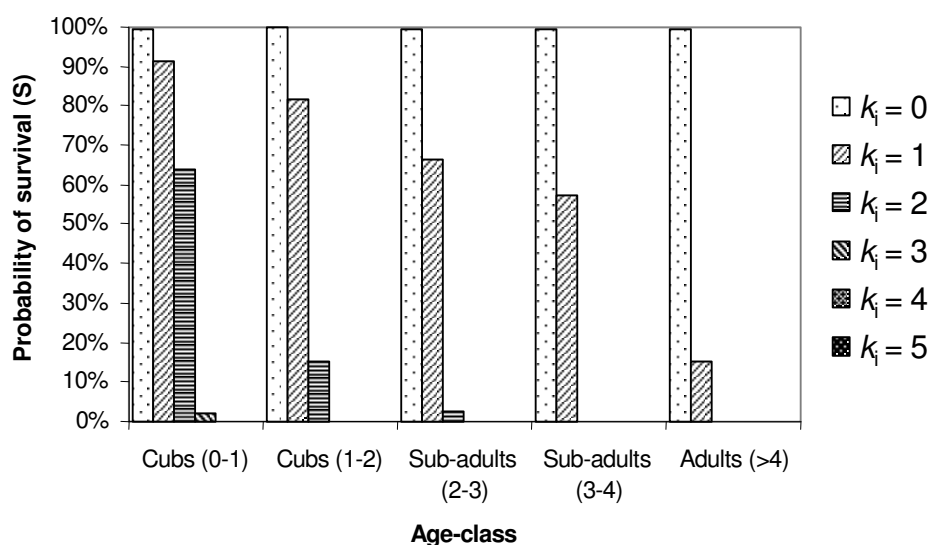


Figure 11. The survival probability (S) of the model sub-population with mean fecundity and birth sex ratio rates, and increasing human-caused mortality (k_i). The sub-population had only a 15% probability of survival above the MVAP when a minimum of one adult was persecuted annually.

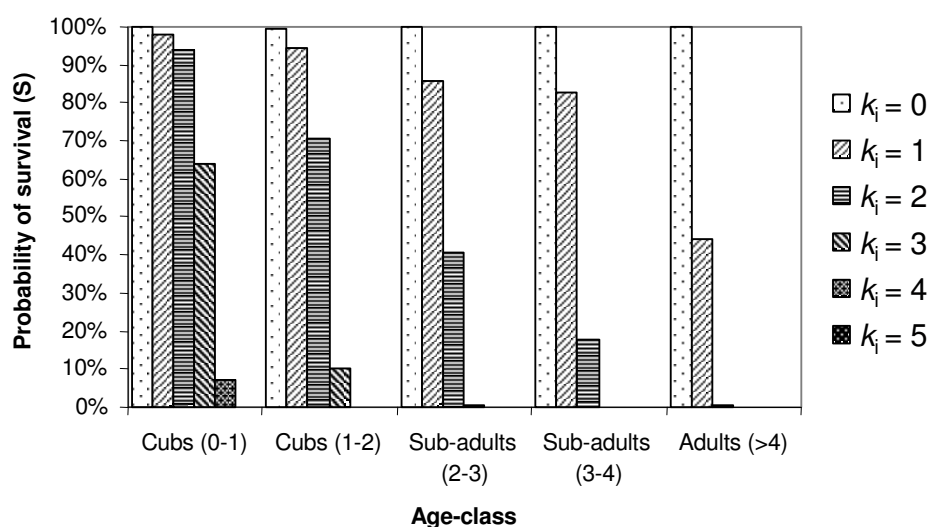


Figure 12. The survival probability (S) of the model sub-population with a mean birth sex ratio (0.50) and extreme upper fecundity (0.87), and increasing human-caused mortality (k_i). The survival probability was only 44% when one adult female was persecuted annually.

Even with the most optimistic fecundity rate and birth sex ratio, the maximum survival probability was 78 and 13% respectively when only one or two adults were persecuted annually (Figure 13, Appendix Table C.13). The model sub-population was unable to sustain itself with the most pessimistic parameter values, even when human-caused mortality was zero (Appendix Table C.13).

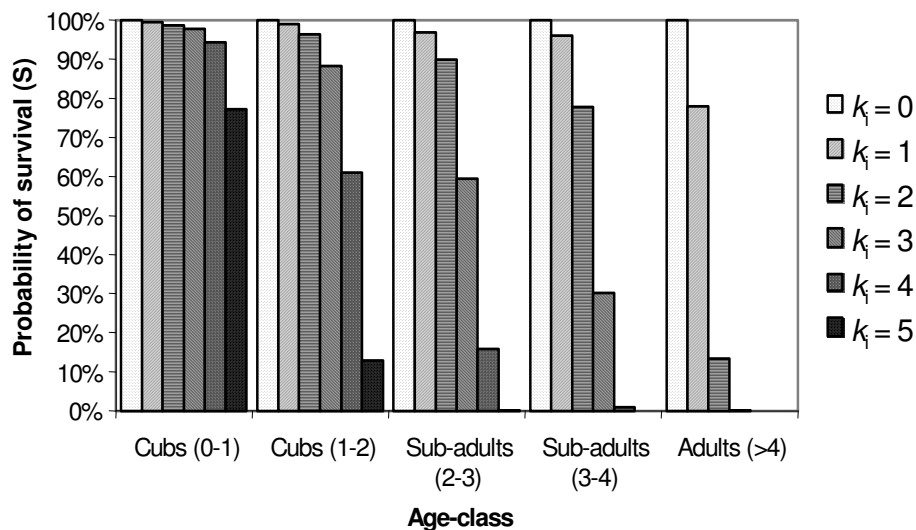


Figure 13. The survival probability (S) of the model sub-population with the most optimistic parameter values, *i.e.* a combination of the upper extreme rates for birth sex ratio and fecundity. The survival probability was 78% when only one adult was persecuted annually.

CHAPTER 5: DISCUSSION

The long-term extent of human-caused mortality sustained by the lion sub-population in the KTP is unknown, except in recent years for which records of stock-depredation instances are available. These records indicate that at least one adult female (approximately 4%) is killed annually from the sub-population of five prides that have home ranges adjoining livestock farming areas. Details on population parameters of the KTP population are also limited, as are detailed history records of prides, their members, and dynamics. Hence little inference can be made with respect to the viability of the sub-population subject to the current rates of persecution. The models presented here serve to investigate whether a modelled representative of this sub-population is able to sustain the persecution rate with the limited knowledge available. Hence the models were developed using only the most simple population parameters, excluding the more complex components of lion socio-biology. The characteristics of the models make them useful for comparing the effects of changes in age-specific and other parameter values on population responses. Further, by using a range of reasonable hypothetical parameter values, where real data is lacking, an attempt is made to gain insight into the problem being addressed, with suggestions for population management. It also emphasises those data that are currently lacking and that need to be addressed by further field research.

Both a deterministic and stochastic model was developed in the course of this study, although a stochastic approach is generally recommended for small populations (Grier, 1980; Piper, 1994), where variance in the behaviour of the system becomes increasingly important (Starfield & Bleloch, 1986). Deterministic models are more reliable for large populations where probability is spread across the population with the effect thereof becoming more predictable (Grier, 1980). An initial deterministic model was nevertheless set up on spreadsheet to display the sequence of the birth-and-death process, with mean age-specific survival and fecundity rates applied annually for a 50-year duration. The deterministic model was developed first because it is easier to implement than a stochastic model, and because it leads, at the very least, to an initial understanding of the system dynamics. The model was then modified to incorporate stochasticity, by introducing variable survival rates and environmental stochasticity on an annual basis. Demographic stochasticity, due to intrinsic variations between individuals (Gilpin & Soulé, 1986), was not considered in the model, primarily because of a lack of detailed empirical data on demographic parameters.

5.1 Sensitivity of natural survivorship

Sensitivity analysis of natural survival rates demonstrated the importance of adult female survivorship to population viability. Although the results of the deterministic model suggests that the adult segment of the model sub-population can sustain a 5% reduction in annual survival rates, in the average case scenario (Figure 8), this is not the case in the stochastic model. The latter presents a more realistic scenario in terms of environmental stochasticity, where a 5% reduction in annual adult survival rates results in only a 12% probability of the model sub-population surviving above the MVAP. The results of the deterministic and stochastic models are, however, not contradictory, as a high survival probability can be expected when environmental conditions remain fixed at mean rates between years, as in the former model. While a 1% decrease in adult survival rate had no marked effect on the viability of the model sub-population in the stochastic model, a decrease between 2 and 3% resulted in a 78 and 58% survival probability (Table 5). The viability of the model sub-population is thus sensitive to small perturbations in this parameter. The importance of adult survival, as illustrated by the models, is typical for numerous moderate- to long-lived animal species (Wu & Botkin, 1980; Crouse *et al.*, 1987; Caswell, 1989; Crooks *et al.*, 1997). However, while adult survival is considered crucially important, the survivorship of younger age-classes should not be underestimated. Extremely high cub mortality in cheetah, for example, could affect populations negatively (Crooks *et al.* 1997).

Sensitivity analysis of female fecundity and birth sex ratio showed that these parameters were insensitive to changes in their values. According to Demetrius (1969), reduced mortality in any age class of a population would increase population growth rate more than an increase in reproductive rate of a perennial species. The role that these parameters may play in determining population persistence could therefore be regarded as negligible compared to adult survivorship. Their insensitivity further suggests that moderate changes in these, such as compensatory changes in response to increasing persecution, are unlikely to have any marked effect on the modelled sub-population's viability. However, while accurate details regarding these parameters may be desirable to obtain, park management should focus on obtaining accurate survival estimates for adults, the most sensitive population parameter

5.2 Response to persecution

With respect to persecution rates, the adult female age-class was the most sensitive, as expected, followed by sub-adults (3–4 years) and then cubs (0–1 years), in that order. A positive correlation would be expected between age and sensitivity to perturbations, as annual

survival rates increase with increasing age in lions (Schaller, 1972; Bertram, 1973), at least until early adulthood. Thus, apart from adult females, independent sub-adult females (3–4 years) could be considered a sensitive age-class, which recruit annually into the adult sub-population. Hence persecution of independent sub-adults may be an undesirable outcome of boundary transgressions.

The simulations subjected to the extreme rates of fecundity and birth sex ratio, under the best- and average-case scenario, provide the most conclusive results regarding sustainable persecution rates (Table C.8). While such extreme parameter rates are possible for short durations, it is unlikely that prides would simultaneously exhibit similar rates, or that these could be maintained for long periods in the real sub-population. When considering the most optimistic scenario using these extreme rates, the P_{\max} threshold for the model sub-population lies between 2 and 3 adult females annually depending on the prevailing ecological scenario. Since the model population cannot sustain an annual loss of more than 3 adult females under these utopian conditions, it can be considered unlikely that this persecution rate is sustainable in the real sub-population where ecological conditions fluctuate regularly. When considering the worst-case scenario with fecundity and sex ratio rates at their lower extremes, the P_{\max} value for all age-classes is zero. While these scenarios are unrealistic, as fixed ecological conditions between years cannot be expected in reality, and parameters are at their mean in the long-term (Schaller, 1972; Packer & Pusey, 1987), they do highlight the thresholds of sustainable persecution. If persecution were sustained under the most pessimistic scenario, then it could be assumed that the real sub-population would sustain similar, and possibly higher persecution rates. As the model sub-population is unable to sustain itself in the most optimistic scenario, then the annual persecution rate of 2 to 3 adults could be considered unsustainable in the real sub-population. Using the stochastic model under the most optimistic scenario (with upper extreme rates of birth sex ratio and fecundity), the highest achievable survival probability, where one adult female was persecuted annually, was 78%. Thus under the most optimistic, yet most realistic stochastic conditions, the current persecution rate of one adult annually (or 4% of the adult segment), appears to be unsustainable in the model sub-population. With the parameters at their mean rates, the survival probability was only 12%. While higher persecution rates can be sustained by the model sub-population when the birth sex-ratio is female-biased, or when fecundity is at its upper extreme, these parameters are generally at their mean values over the long-term for lions. Hence, where the modelled sub-population is unable to sustain persecution with a female-biased sex ratio or upper limit

fecundity rate, for all of the simulation years, it is unlikely that a positive temporary change in these parameters may prevent a decline in the real sub-population.

Empirical evidence suggests that persecution mortalities among large felids may not necessarily depress their densities, provided that less than 10 to 25% of the population is removed annually (Lindzey *et al.*, 1992; 1994). This may be possible if the effect of persecution is likely to be partially compensatory, rather than additive, such as when age-classes, which generally experience naturally high mortality, are killed (Karanth & Stith, 1999). This could be an explanation for the higher sustainable persecution rates for younger female age-classes. The high survival rate of adult lionesses suggests that persecution would most probably have an additive effect, resulting in increased sensitivity to persecution. The threshold levels set by habitat quality and reproductive potential of the species may also cause the decline of a population if persecution exceeds these limitations (Martin & Meulenaer, 1988). Furthermore, Karanth & Stith (1999) found that moderate sized tiger (*Panthera tigris*) populations are able to sustain a 7% persecution rate of juvenile, transient, and breeders of both sexes, but that a persecution rate of 10% results in a moderately declining population trend. This further illustrates the sensitivity of felid populations to perturbations, with only low persecution rates being sustainable. Further, the results presented here are substantiated by matrix models (Van Vuuren *et al.*, in press) incorporating identical population parameters as used in the spreadsheet models. They concluded that a persecution rate of one adult annually from a sub-population was unsustainable under a specified set of conditions. Furthermore, for each P_{\max} value determined, the time to MVAP indicates that a population decline might be gradual, and could probably go undetected for several years before the MVAP is reached. Hence management should be aware that a population decline might not necessarily be rapid and conspicuous. The KTP lion population appears to exhibit population fluctuations in response to environmental variables, with periods of minimal and maximal population densities lasting for a number of years (Funston, 2001). Successive years of low population density may be attributed to low survival rates, resulting from unfavourable environmental conditions for lions. The lion population in the southwestern KTP exhibited a concerning decline in 1996 following non-violent mortality (Castley *et al.*, 2001), but has since recovered to some extent (Funston, 2001). Park management should thus be able to distinguish between environmental related and anthropogenic induced population declines in the KTP lion population.

When compared to lion populations occurring in the mesic environments of southern Africa, it appears that the Kalahari lion population may be markedly less resilient to human-caused perturbations. From field trials in the Kruger National Park, Smuts (1978a) determined that lions responded in two ways following extensive lion cropping exercises, namely by extension of ranges by surrounding groups not culled, and by increased reproductive success. Between 63 and 100% of lions of all ages were removed. Where lions were cropped gradually from small areas there was increased reproductive success compared to when large scale short-term cropping was undertaken. In the latter strategy, large vacant areas were created, which attracted foreign lions that initially interacted aggressively, which may have resulted in reduced fecundity and cub survival. Where only a few individuals at a time, or when one pride was removed, less vacant areas were created resulting in a lower influx of foreign lions. However, irrespective of which cropping strategy was imposed, the number of lions recovered to their original density within a relatively short period of time, mainly due to infiltration from surrounding areas and from increased reproduction. The majority of lions that recolonised areas, relative to their abundance in the population prior to cropping, were sub-adults, followed by adults (Smuts, 1978a). Population models used previously for simulating lion cropping strategies in these mesic environments, either to prevent the decline of ungulate prey populations (*e.g.* Starfield *et al.*, 1981a; b) or to reduce incidents of livestock depredation by transgressing lions (Venter & Hopkins, 1988), also suggest that a far greater proportion of adult females can be removed from the prides with minimal impact on the population size. Venter and Hopkins (1988) reported that the removal of 50% of adult pride females from 50% of the prides resulted in only a 0 to 20% reduction in the lion population remaining in the conservation area. The resilience of the KTP model sub-population to instantaneous but severe perturbations was relatively high in most of the scenarios tested, especially when ecological conditions were consistently average or good, or when parameters such as birth sex ratio and fecundity were at their upper limits. However, when these parameters were at their lower limits, resilience was substantially retarded. While favourable ecological conditions may be beneficial for recovery after a perturbation, this is not likely to be the case in the long-term under a fluctuating regime of average, good and poor ecological years. The combined effect of continual annual persecution, and a severe perturbation, especially where as much as 40% of the adult females are removed, may have serious negative effects on the model sub-populations' ability to recover. A rapid recovery would require that there is sufficient recruitment, in the majority of younger female age-classes, to compensate for adult losses. Such a high level of recruitment potential may only be possible following several years of very favourable ecological conditions, which could be considered unlikely in an arid

environment such as the southern Kalahari. The limitations imposed by habitat quality, reproductive potential (Martin & Meulenaer, 1988), as well as the low population density and low fecundity (Funston, 2001), may thus inhibit a rapid response by Kalahari lions to population perturbations. Fertility, for example, is indeed higher in the more mesic areas of southern Africa, where females produce on average three offspring every two years (annual fecundity rate of 1.5 cubs per female (Starfield & Bleloch, 1986), compared to the mean of 0.67 for females in the KTP (Funston, 2001). The extinction of the sub-population, however, does not imply that the entire KTP population is at risk of extinction, as lions from areas outside the sub-population may invade large vacant areas to take up residence. The capacity of the KTP population, beyond the boundaries of the sub-population, to serve as a reservoir of immigrating lions into the latter is unknown, and may warrant further investigation.

5.3 Strengths and weaknesses of the models

The models were constructed with the objective of determining whether the sub-population is able to sustain the current persecution rate to which it is subjected. In order to achieve this objective, some important aspects of lion behaviour and ecology were omitted, for the sake of simplicity. However, despite the omission of behavioural aspects, the models are strengthened to some extent because of these omissions. The models are generally robust in terms of population processes and simulation, while highlighting those parameters essential to population survival by virtue of their sensitivities. Further, both deterministic and stochastic approaches were taken, generating comparable results with respect to parameter sensitivities and population responses to persecution scenarios. A particular advantage of the models is the ease with which what-if scenarios can be investigated, to determine thresholds of population viability with respect to changes in population parameters. Conversely, the models may be unable to monitor or detect socio-ecological changes in the sub-population, which may be of particular importance if lion persecution were to cause changes in social behaviour (Yamazaki, 1996; Whitman & Packer, 1997). The loss of adult males from a pride, such as through persecution, may result in young cubs succumbing to infanticide when new adult males become the pride owners (Schaller, 1972; Packer *et al.*, 1988). Persecution of territorial male lions may thus also have a detrimental effect on population growth and viability (Starfield *et al.*, 1981a; Whitman & Packer, 1997).

Model stochasticity was incorporated in a very crude manner, particularly since the actual relationship between rainfall, prey density and lion survival rates is not clearly understood in the southern Kalahari. The model could therefore be improved by the incorporation of a more

accurate correlation between rainfall and lion survival rates, as well as accurate or quantitatively determined lion survival rates, particularly for adults. However, survival rates of long-lived species are generally difficult to obtain (Lindzey *et al.*, 1988). The models do highlight the importance of this parameter though, providing direction for future studies of the species in the region.

CONCLUSION

The KTP lion sub-population has been subjected to persecution for several decades, although no detailed records exist to quantify the exact extent or impact of such losses. Only recently has there been an improvement in the record keeping of the numbers of boundary-transgressing lions shot. From 1997 to 2000 a total of four adult lionesses from boundary prides were shot while transgressing, which, according to the models, is possibly unsustainable in the long-term. While the area still exhibits a healthy lion sub-population, which appears in most respects to be unaffected by persecution (Funston, 2001), the model results give rise to a number of hypotheses. The models did not attempt to estimate accurate sustainable persecution rates for the sub-population, but rather highlight possible thresholds. In the deterministic model, an annual persecution rate exceeding 2 to 3 adult females is considered unsustainable under utopian conditions, suggesting that this may be, an extreme maximum sustainable persecution rate in the real sub-population. In turn, the stochastic model suggests that the persecution of one adult annually is unsustainable. Due to a lack of records regarding boundary transgressions by lions during the preceding two to three decades, it is possible that the sub-population has sustained a lower persecution rate than one adult female annually, until recently. Such a scenario might be sustainable, which would account for the current status of the sub-population, which appears largely unaffected by persecution. The apparent absence of emigration from the sub-population in recent years, suggests that recruitment of sub-adults possibly compensates for the current rate of adult persecution, thereby equalising population growth. According to the models, this would only be possible if adults have not been persecuted every year in recent decades. Alternatively, the parameter estimates used in the models may have a marked effect on model results. The sensitivity of adult survival, for example, indicates that even minor changes in this parameter may have a marked influence on the viability of the model sub-population. In contrast, insensitive parameters such as birth sex ratio, fecundity and survival rates of younger age-classes are less likely to influence population viability. Management should therefore attempt an accurate estimation of adult survival rates, and also initiate a thorough investigation of persecuted versus un-persecuted prides with respect to size, fecundity and sub-adult emigration. This may elucidate those population parameters that possibly have a compensatory effect on prides subjected to persecution.

REFERENCES

- Acocks, J.P.H. (1988). Veld types of South Africa. *Mem. Bot. Surv. S. Afr.*, **57**, 1-146.
- Anderson, J.L. (1981). The re-establishment and management of a lion *Panthera leo* population in Zululand, South Africa. *Biol. Conserv.*, **19**, 107-117.
- Bertram, B.C.R. (1973). Lion population regulation. *E. Afr. Wildl. J.*, **11**, 215-225.
- Bertram, B.C.R. (1975). Social factors influencing reproduction in wild lions. *J. Zool. Lond.*, **177**, 463-482.
- Bertram, B.C.R. (1979). Serengeti predators and their social systems. In *Serengeti: Dynamics of an ecosystem*, ed. A.R.E. Sinclair & M. Norton-Griffiths. University of Chicago Press, Chicago, Illinois, pp. 221-248.
- Bullard, J.E., Thomas, D.S.G., Livingstone, I. & Wiggs, G.F.S. (1995). Analysis of linear sand dune morphological variability, southwestern Kalahari Desert. *Geomorphology*, **11**, 189-203.
- Castley, J.G., Knight, M.H., Mills, M.G.L. & Thouless, C. (2001). Estimation of the lion population in the Kalahari Gemsbok National Park using a mark-resighting exercise, with notes on population structure. *Afr. Zool.*, **37**, 27-34.
- Caswell, H. (1989). *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts.
- Caughley, G., & Gunn, A. (1996). *Conservation biology in theory and practice*. Blackwell Science, Cambridge.
- Coe, M.J., Cumming, D.H. & Phillipson, J. (1976). Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia*, **22**, 341-354.
- Creel, S. & Creel, N.M. (1997). Lion density and population structure in the Selous Game Reserve: evaluation of hunting quotas and offtake. *Afr. J. Ecol.*, **35**, 83-93.

- Crooks, K.R., Sanjayan, M.A. & Doak, D.F. (1997). New insights on cheetah conservation through demographic modelling. *Conserv. Biol.*, **12**, 889-895.
- Crouse, D., Crowder, L. & Caswell, H. (1987). A stage-based population model for loggerhead sea turtles and implications for conservation. *Ecology*, **68**, 1412-1423.
- Demetrius, L. (1969). The sensitivity of population growth rate to perturbations in the life cycle components. *Math. Biosci.*, **4**, 129-136.
- Deshmukh, I.K. (1984). A common relationship between precipitation and grassland peak biomass for East and southern Africa. *Afr. J. Ecol.*, **22**, 181-186.
- Dunham, K.M. (1992). Response of a lion (*Panthera leo*) population to changing prey availability. *J. Zool. Lond.*, **227**, 330-333.
- East, R. (1984). Rainfall, soil nutrient status and biomass of large African savanna mammals. *Afr. J. Ecol.*, **22**, 245-270.
- Eloff, F.C. (1973). Lion predation in the Kalahari Gemsbok National Park. *J. S. Afr. Wildl. Manage. Assoc.*, **3**, 59-63.
- Eloff, F.C. (1980). Cub mortality in the Kalahari lion *Panthera leo vernayi*. *Koedoe*, **23**, 163-170.
- Eloff, F.C. (1984). Food ecology of the Kalahari lion *Panthera leo vernayi*. *Koedoe*, **27** (Suppl.), 249-258.
- Funston, P.J. (2001). Kalahari Transfrontier Lion Project. Population-ecology and long term monitoring of a free-ranging population in an arid environment. Unpublished report, Endangered Wildlife Trust, Johannesburg.
- Funston, P.J., Mills, M.G.L., Biggs, H.C. & Richardson, P.R.K. (1998). Hunting by male lions: Ecological influences and socioecological implications. *Anim. Behav.*, **56**, 1333-1345.

- Funston, P.J., Mills, M.G.L. & Biggs, H.C. (2001). Factors affecting the hunting success of male and female lions in the Kruger National Park. *J. Zool. Lond.*, **253**, 419-431.
- Gaona, P., Ferreras, P. & Delibes, M. (1998). Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). *Ecol. Monogr.*, **68**, 349-370.
- Gilpin, M.E. & Soulé, M.E. (1986). Minimum viable populations: processes of species extinction. In *Conservation Biology: the science of scarcity and diversity*, ed. M.E. Soulé. Sinauer Associates, Sunderland, Massachusetts, pp. 19-34.
- Grier, J.W. (1980). Ecology: a simulation model for small populations of animals. *Creative Computing*, **6** (7), 116-121.
- Hanks, J., Densham, W.D., Smuts, G.L., Jooste, J.F., Joubert, S.C.J., le Roux, P. & Milstein, P.I.S. (1981). Management of locally abundant mammals: the South African experience. In *Problems in management of locally abundant wild animals*, ed. P.A. Jewel & S. Holt. Academic Press, New York, pp. 21-55.
- Hanby, J.P. & Bygott, J.D. (1979). Population changes in lions and other large predators. In *Serengeti: dynamics of an ecosystem*, ed. A.R.E. Sinclair & M. Norton-Griffiths. University of Chicago Press, Chicago, pp. 249-262.
- Hanby, J.P., Bygott, J.D. & Packer, C. (1995). Ecology, demography, and behavior of lions in two contrasting habitats: Ngorongoro Crater and the Serengeti Plains. In *Serengeti II: dynamics, management, and conservation of an ecosystem*, ed. A.R.E. Sinclair & P. Arcese. University of Chicago Press, Chicago, pp. 315-331.
- Hilborn, R. & Sinclair, A.R.E. (1979). A simulation of the wildebeest population, other ungulates, and their predators. In *Serengeti: dynamics of an ecosystem*, ed. A.R.E. Sinclair & M. Norton-Griffiths. University of Chicago Press, Chicago, pp. 287-309.
- Holling, C.S. (1978). Adaptive Environmental assessment and management. Wiley, Chichester.

- Huntley, B.J. (1982). Southern African savannas. In *Ecology of tropical savannas*, ed. B.J. Huntley & B.H. Walker. Ecological Studies 42. Springer-Verlag, Berlin, pp. 101-119.
- Jackson, L.J, Trebitz, A.S. & Cottingham, K.L. (2000). An introduction to the practice of ecological modelling. *BioScience*, **50**, 694-706.
- Jordan, D.W. & Smith, P. 1988. Non-linear ordinary differential equations. Clarendon Press, University of Oxford, Oxford.
- Karanth, K.U. & Stith, B.M. (1999). Prey depletion as a critical determinant of tiger population viability. In *Riding the tiger: tiger conservation in human-dominated landscapes*, ed. J. Seidensticker, S. Christie & P. Jackson. Cambridge University Press, Cambridge, pp. 100-113.
- Knight, M.H. (1991). Ecology of the Gemsbok *Oryx gazella gazella* (Linnaeus) and Blue Wildebeest *Connochaetes taurinus* (Burchell) in the southern Kalahari. PhD thesis, University of Pretoria, Pretoria.
- Knight, M.H. (1995). Drought-related mortality of wildlife in the southern Kalahari and the role of man. *Afr. J. Ecol.*, **33**, 377-394.
- Lancaster, N. (1988). Development of linear dunes in the southwestern Kalahari, Southern Africa. *J. Arid Environ.*, **14**, 233-244.
- Leistner, O.A. (1959). Notes on the vegetation of the Kalahari Gemsbok National Park with special reference to its influence on the distribution of antelopes. *Koedoe*, **2**, 128-151.
- Leistner, O.A. (1967). The plant ecology of the southern Kalahari. *Mem. Bot. Surv. S. Afr.*, **38**, 1-172.
- Leistner, O. A. & Werger, M. J. A. (1973). Southern Kalahari phytosociology. *Vegetatio*, **28** (5 - 6), 353 - 399.
- Lindzey, F.G, Ackerman, B.B., Barnhurst, D. & P. Hemker. (1988). Survival rates of mountain lions in southern Utah. *J. Wildl. Mgmt.*, **52**, 664-667.

- Lindzey, F.G., van Sickle, W.D., Laing, S.P. & Mecham, C.S. (1992). Cougar population response to manipulation in southern Utah. *Wildl. Soc. Bull.*, **20**, 224-227.
- Lindzey, F.G., van Sickle, W.D., Ackerman, B.B, Barnhurst, D., Hemker, T.P. & Laing, S.P. (1994). Cougar population dynamics in southern Utah. *J. Wildl. Mgmt.*, **58**, 619-624.
- Martin, R.B. & de Meulenaer, T. (1988). Survey of the status of the leopard *Panthera pardus* in Sub-Saharan Africa. CITES report, Switzerland.
- Mills, M.G.L. (1984). Prey selection and feeding habits of the larger carnivores in the southern Kalahari. *Koedoe*, **27** (Suppl.), 281-294.
- Mills, M.G.L. (1990). Kalahari Hyaenas. Comparative behavioural ecology of two species. Unwin Hyman, London.
- Mills, M.G.L. (1991). Conservation management of large carnivores in Africa. *Koedoe*, **34**, 81-90.
- Mills, M.G.L., Wolf, P., Le Riche, E.A.N. & Meyer, I.J. (1978). Some population characteristics of the lion (*Panthera leo*) in the Kalahari National Park. *Koedoe*, **21**, 163-171.
- Mills, M.G.L. & Retief, P.F. (1984). The response of ungulates to rainfall along the riverbeds of the southern Kalahari. *Koedoe*, **27** (Suppl.), 129-142.
- Mills, M.G.L. & Shenk, T.M. (1992). Predator-prey relationships: the impact of lion predation on wildebeest and zebra populations. *J. Anim. Ecol.*, **61**, 693-702.
- Mills, M.G.L., Biggs, H.C. & Whyte, I.J. (1995). The relationship between rainfall, lion predation and population trends in African herbivores. *Wildl. Res.*, **22**, 75-88.
- Myers, N. (1986). Conservation of Africa's cats: problems and opportunities. In *Cats of the world: biology, conservation and management*, ed. S.D. Miller & D.D. Everett. National Wildlife Federation, Washington D.C., pp. 437-446.

- Norton, P.M. (1989). Population dynamics of mountain reedbuck on three Karoo nature reserves. PhD thesis, University of Stellenbosch, Stellenbosch.
- Norton, P.M. (1994). Simple spreadsheet models to study population dynamics, as illustrated by a mountain reedbuck model. *S. Afr. J. Wildl. Res.*, **24**, 73-81.
- Nowell, K. & Jackson, P. (eds) (1996). Wild Cats. Status survey and conservation action plan. IUCN, Gland.
- O'Brien, S.J., Martenson, J.S., Packer, C., Herbst, L.H., de Vos, V., Joslin, P., Wildt, D.E. & Bush, M. (1987). Biochemical genetic variation in geographic isolates of African and Asiatic lions. *Nat. Geog. Res.*, **3**, 114-124.
- Packer, C. (1986). The ecology of sociality in Felids. In *Ecological aspects of social evolution*, ed. D.I. Rubenstein & W.R. Wrangham. Princetown University Press, Princeton, New Jersey, pp. 429-451.
- Packer, C. & Pusey, A.E. (1984). Infanticide in carnivores. In *Infanticide: Comparative and evolutionary perspectives*, ed. G. Hausfater & S.B. Hrdy. Aldine, Hawthorne, New York, pp. 31-42.
- Packer, C. & Pusey, A.E. (1987). Intrasexual cooperation and the sex ratio in African lions. *Am. Nat.*, **130**, 636-642.
- Packer, C. & Pusey, A.E. (1993). Dispersal, kingships and inbreeding in African lions. In *The natural history of inbreeding and outbreeding: theoretical and empirical perspectives*, ed. N.W. Thornhill. University of Chicago Press, Chicago, pp. 375-391.
- Packer, C., Herbst, L., Pusey, A.E., Bygott, J.D., Hanby, J.P., Cairns, S.J., & Borgerhoff-Mulder, M. 1988. Reproductive success in lions. In *Reproductive success*, ed. T.H. Clutton-Brock. Chicago University Press, Chicago, pp. 363-383.
- Packer, C., Scheel, D. & Pusey, A.E. (1990). Why lions form groups: food is not enough. *Am. Nat.*, **136**, 1-19.

- Pimm, S.L. (1991). The balance of nature? Ecological issues in the conservation of species and communities. The University of Chicago Press, Chicago.
- Piper, S.E. (1994). Mathematical demography of the Cape vulture. PhD thesis, University of Cape Town, Cape Town.
- Pusey, A.E. & Packer, C. (1987). The evolution of sex-biased dispersal in lions. *Behaviour*, **101**, 275-310.
- Pusey, A.E. & Packer, C. (1994). Non-offspring nursing in social carnivores: minimizing the costs. *Behav. Ecol.*, **5**, 362-374.
- Quigley, H.B. & Crawshaw, P.G. (1992). A conservation plan for the jaguar *Panthera onca* in the Pantanal region of Brazil. *Biol. Conserv.*, **61**, 149-157.
- Rudnai, J. (1973). Reproductive biology of lions (*Panthera leo massaica* Neumann) in Nairobi National Park. *E. Afr. Wildl. J.*, **11**, 241-253.
- Ruggiero, R.G. (1991). Prey selection of the lion (*Panthera leo* L.) in the Manovo-Gounda-St. Floris National Park, Central African Republic. *Mammalia*, **55**, 23-33.
- Rutherford, M.C. (1980). Annual plant production-precipitation relations in arid and semi-arid regions. *S Afr. J. Sci.*, **76**, 53-56.
- Schaller, G.B. (1972). The Serengeti lion: a study of predator-prey relations. University of Chicago Press, Chicago.
- Scheel, D. (1993). Profitability, encounter rates, and prey choice of African lions. *Behav. Ecol.*, **4**, 90-97.
- Scholz, R.J. & Walker, B.H. (1993). An African savanna: synthesis of the Nylsvlei Study. Cambridge University Press, Cambridge.
- Seely, M.K. (1978). Grassland productivity: the desert end of the curve. *S Afr. J. Sci.*, **74**, 295-297.

- Sibly, R.M. & Calow, P. (1986). *Physiological ecology of animals: an evolutionary approach*. Blackwell Scientific Publications, Oxford.
- Sinclair, A.R.E. (1979). The eruption of the ruminants. In *Serengeti: dynamics of an ecosystem*, ed. A.R.E. Sinclair & M. Norton-Griffiths. University of Chicago Press, Chicago, pp. 82-103.
- Skarpe, C. (1986). Plant community structure in relation to grazing and environmental changes along a north-south transect in the western Kalahari. *Vegetatio*, **68**, 3-18.
- Smuts, G.L. (1976). Population characteristics and recent history of lions in two parts of the Kruger National Park. *Koedoe*, **19**, 153-164.
- Smuts, G.L. (1978a). Effects of population reduction on the travels and reproduction of lions in Kruger National Park. *Carnivore*, **1**, 61-72.
- Smuts, G.L. (1978b). Interrelations between predators, prey, and their environment. *BioScience*, **28**, 316-320.
- Smuts, G.L., Hanks, J. & Whyte, I.J. (1978). Reproduction and social organisation of lions from the Kruger National Park. *Carnivore*, **1**, 17-28.
- Stander, P.E. (1990). A suggested management strategy for stock-raiding lions in Namibia. *S. Afr. J. Wildl. Res.*, **20**, 53-60.
- Stander, P.E. (1991). Demographics of lions in the Etosha National Park. *Madoqua*, **18**, 1-9.
- Stander, P.E. (1993). Conservation of African carnivores in a developing world. In *Wildlife ranching: a celebration of diversity*, ed. W. Van Hoven & H. Ebedes. Proceedings of the third International Wildlife Ranching Symposium, Pretoria, pp. 368-372.
- Stander, P.E. (1997). The ecology of lions and conflict with people in north-eastern Namibia. In *Proceedings of a symposium on lions and leopards as game ranch animals*, ed. J. Van Heerden. Onderstepoort, Pretoria, pp. 10-17.

- Stander, P.E. & Albon, S.D. (1993). Hunting success of lions in a semi-arid environment. *Symp. zool. Soc. Lond.*, **65**, 127-143.
- Starfield, A.M., Shiell, J.D. & Smuts, G.L. (1981*a*). Simulation of lion control strategies in a large game reserve. *Ecol. Model.*, **13**, 17-28.
- Starfield, A.M., Furniss, P.R. & Smuts, G.L. (1981*b*). A model of lion population dynamics as a function of social behaviour. In *Dynamics of large mammal populations*, ed. C.W. Fowler. John Wiley & Sons, Chichester, pp. 121-134.
- Starfield, A.M. & Bleloch, A.L. (1986). *Building models for conservation and wildlife management*. Macmillan, New York.
- Thresher, P. (1981). The economics of a lion. *Unasylva*, **33**, 34-35.
- Trivers, R.L. & Willard, D.E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. *Science*, **179**, 90-91.
- Van der Meulen, J.H. (1977). Notes on the capture and translocation of stock raiding lions in north eastern and north western Rhodesia. *S. Afr. J. Wildl. Res.*, **7**, 15-17.
- Van Orsdol, K.G. (1982). Ranges and food habits of lions in Rwenzori National Park, Uganda. *Symp. Zool. Soc. Lond.*, **49**, 325-334.
- Van Orsdol, K.G., Hanby, J.P. & Bygott, J.D. (1985). Ecological correlates of lion social organization (*Panthera leo*). *J. Zool.*, **206**, 97-112.
- Van Rooyen, N., Van Rensburg, D. J., Theron, G. K. & Bothma, J. Du P. (1988). A check list of flowering plants of the Kalahari Gemsbok National Park. *Koedoe*, **31**, 115-135.
- Van Rooyen, N., Bezuidenhout, D., Theron, G.K. & Bothma, J. Du P. (1990). Monitoring of the vegetation around artificial watering points (windmills) in the Kalahari Gemsbok National Park. *Koedoe*, **33**, 63-88.

- Van Rooyen, T.H. (1984). The soils of the Kalahari Gemsbok National Park. *Koedoe*, **27**, Suppl.), 45-61.
- Van Vuuren, J.H., Herrmann, E. & Funston, P.J. (in press). Lions in the Kgalagadi Transfrontier Park: modelling the effect of human-caused mortality. *Int. Trans. Operational Res.*
- Venter, J. & Hopkins, M.E. (1988). Use of a simulation model in the management of a lion population. *S. Afr. J. Wildl. Res.*, **18**, 126-130.
- Verlinden, A. (1998). Seasonal movement patterns of some ungulates in the Kalahari ecosystem of Botswana between 1990 and 1995. *Afr. J. Ecol.*, **36**, 117-128.
- Verlinden, A. & Masogo, R. (1997). Satellite remote sensing of habitat suitability for ungulates and ostrich in the Kalahari of Botswana. *J. Arid. Environs.*, **35**, 563-574.
- Walker, B.H., Emslie, R.H., Owen-Smith, R.N. & Scholes, R.T. (1987). To cull or not to cull: lessons learnt from a southern African drought. *J. Appl. Ecol.*, **24**, 381-401.
- Werger, M. J. A. (1978). Vegetation structure in the southern Kalahari. *J. Ecol.*, **66**, 933-941.
- Whitman, K. & Packer, C. (1997). The effect of sport hunting on the social organisation of the African lion (*Panthera leo*). In *Proceedings of a symposium on lions and leopards as game ranch animals*, ed. J. Van Heerden. Onderstepoort, Pretoria, pp. 177-183.
- Wu, L.S. & Botkin, D.B. (1980). Of elephants and men: a discrete, stochastic model for a long-lived species with complex life histories. *Am. Nat.*, **116**, 831-849.
- Yamazaki, K. (1996). Social variation of lions in a male-depopulated area in Zambia. *J. Wildl. Manage.*, **60**, 490-497.

APPENDIX A: LAYOUT OF MODEL IN SPREADSHEET

	A	B	C	D	E	F	G	H	I	J	K	L					
1						Random no.	0.73	0.86	0.86	0.22	0.53	0.05	0.99				
2						Annual rainfall	225	275	275	125	175	75	575				
3																	
4											Year (1 to 50)	1	2	3	4	5	
5											Ecol. condition	good	good	average	poor	poor	
6	Annual survival rates																
7	Age-class		Lower	Mean	Upper	NATURAL MORTALITY											
8	Cubs (0-1)		0.10	0.50	0.60	Cubs (0-1)	3	4	5	4	1	1					
9	Cubs (1-2)		0.30	0.75	0.90	Cubs (1-2)	3	3	4	4	1	0					
10	Sub-adult (2-3)		0.60	0.90	0.95	Sub-adult (2-3)	3	3	3	4	2	1					
11	Sub-adult (3-4)		0.85	0.95	0.97	Sub-adult (3-4)	4	3	3	3	3	2					
12	Adult (≥4)		0.95	0.97	0.97	Adult (≥4)	20	23	25	27	27	27					
13						HUMAN-CAUSED MORTALITY											
14	Fecundity		0.67	Cubs (0-1)													
15	Sex ratio		0.50	Cubs (1-2)													
16	Look-up table for rainfall					Sub-adult (2-3)											
17						Sub-adult (3-4)											
18						Adult (≥4)											
19						0.00	75	POST HUMAN-CAUSED MORTALITY									
20						0.10	125	Cubs (0-1)	3	4	5	4	1	1			
21	0.25	175	Cubs (1-2)	3	3	4	4	1	0								
22	0.63	225	Sub-adult (2-3)	3	3	3	4	2	1								
23	0.78	275	Sub-adult (3-4)	4	3	3	3	3	2								
24	0.91	325	Adult (≥4)	20	23	25	27	27	27								
25	0.94	475	BIRTHS														
26	0.97	575	New born		7	8	8	9	9	9							
27						Cubs (0-1)	3	4	5	4	1	1					
28						Cubs (1-2)	3	3	4	4	1	0					
29						Sub-adult (2-3)	3	3	3	4	2	1					
30						Sub-adult (3-4)	4	3	3	3	3	2					
31						Adult (≥4)	20	23	25	27	27	27					

The format of the KTP lion sub-population model (stochastic version) consists of the model input parameters, as displayed in the top left-hand corner of the spreadsheet (cells A5:E14), and the 50 columns containing the annual population processes, starting in column H. The initial start-up population is entered in cells G8:G12. The number of lions removed by persecution are entered in the rows under the process 'Human-caused mortality' (in the above example there is not human-caused mortality, hence the cells are empty). Newborn cubs are added to the population at the end of the year, in row 26. The formulae used are as follows, using column H, the second year of the model, as an example:

```

H1 = RAND()
H2 = VLOOKUP(H1,$A$19:$B$26,2)
H5 = IF(SUM(F2,G2)<330,"poor",IF(SUM(F2,G2)>=475,"good","average"))
H8 = ROUND(IF(H5="poor",G26*$C$8,IF(H5="good",G26*$E$8,G26*$D$8)),0)
H12 = ROUND(IF(G31<=24,SUM(IF(H5="poor",G30*$C$12,IF(H5="good",G30*$E$12,G30*$D$12)),
IF(H5="poor",G31*$C$12,IF(H5="good",G31*$E$12,G31*$D$12))),SUM(G30*((IF(H5="poor",
*$C$12,IF(H5="good",*$E$12,$D$12)))*((29/5)-(G31/5))),IF(H5="poor",G31*$C$12,
IF(H5="good",G31*$E$12,G31*$D$12)))),0)
H20 = ROUND(IF(H8-H14<0,0,H8-H14),0)
H26 = ROUND((H24*$C$14)*$C$15,0)

```

APPENDIX B: MACRO USED IN STOCHASTIC MODEL

```

Sub LionSimModel()

Application.ScreenUpdating = False 'Do not display any changes on screen while macro runs

Dim RangeAdult(Lamda) As Range
Dim Counter As Integer

Worksheets("Simulation results").Range("B4:BB1003").ClearContents
Set RangeAdult = Worksheets("Model").Range("I12:BF12")

Worksheets("Simulation results").Activate 'Set top left cell of sheets as active cell for start of loop
Range("b4").Activate

For Counter = 1 To 1000 'loop to iterate the model 1000 times
    RangeAdult.Copy
    Worksheets("Model"1).EnableCalculation = False
    Worksheets("Simulation results"2).Activate
    ActiveCell.PasteSpecial (xlPasteValues)
    Cells(Counter + 3, 52).Value=Application.WorksheetFunction.Average(Range(Cells
    (Counter + 3, 2), Cells(Counter + 3, 51)))
    Cells(Counter + 3, 53).Value = Application.WorksheetFunction.Min
    (Range(Cells(Counter + 3, 2), Cells(Counter + 3, 51)))
    If Cells(Counter + 3, 53).Value <= 15 Then
        Cells(Counter + 3, 54).Value = _
        Application.WorksheetFunction.Match(15, Range(Cells(Counter + 3,
        2),Cells(Counter + 3, 51)), -1) + 1
    Else: Cells(Counter + 3, 53).Value = "greater"
    End If
    ActiveCell.Offset(1, 0).Activate
    Worksheets("Model"1).EnableCalculation = True
Next Counter

'Copy averaged data for 1000 simulation run to summary sheet
Worksheets("Summary").Activate
ActiveSheet.Range("B1").End(xlDown).Offset(1, 0).Activate 'select first empty cell in col B
Worksheets("Simulation results").Range("az2:Bb2").Copy
Worksheets("Summary").Activate
ActiveCell.PasteSpecial (xlPasteValues)

'activate the worksheet with model again
Worksheets(Model1).Activate
Application.CutCopyMode = False 'remove data from clipboard
Application.ScreenUpdating = True 'display changes on screen again

End Sub

```

The macro in Excel's Visual Basic Editor used to simulate 1000 iterations of the stochastic model for averaging the results during sensitivity analyses and persecution scenarios (Kistner pers. comm.). The macro recorded the number of adult females in each year for all 1000 iterations (in the "Model" worksheet), then pasted these into a separate worksheet ("Simulation results") where results were averaged; including the probability of the sub-population reaching its minimum viable adult population (MVAP) size and 'time to MVAP' in cases when MVAP was reached.

APPENDIX C: TABLES

Table C.1. Sensitivity analysis of lion survival rates in the deterministic model, using the average-case scenario with mean survival rate estimates. Each age-class' survival rate was reduced individually (while keeping other age-class survival rates unchanged) by 1, 5 and 10%, with the number of adult females remaining in the sub-population after fifty years being recorded for all cases when the population survived. Only adult female survival was sensitive to changes, both to a 5 and 10% change, the latter resulting in the population reaching the MVAP within 15 years. Sensitive cases are denoted by an asterix (*).

Age-class	Survival rate	Percent reduction	Resulting parameter	Adult population size after 50 years	Time to MVAP (years)
Cubs (0–1)	0.50	– 1%	0.495	28	-
		– 5%	0.475	27	-
		– 10%	0.450	27	-
Cubs (1–2)	0.75	– 1%	0.743	28	-
		– 5%	0.713	27	-
		– 10%	0.675	27	-
Sub-adults (2–3)	0.90	– 1%	0.891	28	-
		– 5%	0.855	27	-
		– 10%	0.810	27	-
Sub-adults (3–4)	0.95	– 1%	0.941	28	-
		– 5%	0.903	27	-
		– 10%	0.855	27	-
Adults (≥4)	0.97	– 1%	0.960	27	-
		– 5%	0.922	25*	-
		– 10%	0.873	6*	15

Table C.2. Sensitivity analysis of lion survival rates in the deterministic model, using the best-case scenario with upper limit survival rate estimates. Adult female survival was sensitive to a 10% change, but only marginally, while the MVAP was not reached within the 50-year period. Sensitive cases are denoted by an asterix (*).

Age-class	Survival rate	Percent reduction	Resulting parameter	Adult population size after 50 years	Time to MVAP (years)
Cubs (0–1)	0.6	– 1%	0.594	28	-
		– 5%	0.570	28	-
		– 10%	0.540	28	-
Cubs (1–2)	0.9	– 1%	0.891	28	-
		– 5%	0.855	28	-
		– 10%	0.810	28	-
Sub-adults (2–3)	0.95	– 1%	0.941	28	-
		– 5%	0.903	28	-
		– 10%	0.855	28	-
Sub-adults (3–4)	0.97	– 1%	0.960	28	-
		– 5%	0.922	28	-
		– 10%	0.873	28	-
Adults (≥4)	0.97	– 1%	0.960	28	-
		– 5%	0.922	26	-
		– 10%	0.873	25*	-

Table C.3. Sensitivity analysis of fecundity and birth sex ratio in the deterministic model using the average-case scenario. None of these parameters were sensitive to changes in their values.

Percent reduction	Fecundity		Birth sex ratio	
	Resulting parameter	Adult population size after 50 years	Resulting parameter	Adult population size after 50 years
– 1%	0.66	28	0.49	28
– 5%	0.64	27	0.48	27
– 10%	0.60	27	0.45	27

Table C.4. Sensitivity analysis of female fecundity in the stochastic model. This parameter was not sensitive to either a five, 10 or 20% reduction in its mean value of 0.67.

Percent reduction	Resulting parameter	Survival probability	Mean time to MVAP
– 5%	0.64	100%	-
– 10%	0.60	99%	35
– 20%	0.54	99%	34

Table C.5. Sensitivity analysis of birth sex ratio in the stochastic model. This parameter was not sensitive to a 5, 10 or 20% reduction in its mean value of 0.50.

Percent reduction	Resulting parameter	Survival probability	Mean time to MVAP
– 5%	0.48	100%	-
– 10%	0.45	99%	40
– 20%	0.40	98%	28

Table C.6. The maximum sustainable age-specific persecution rates, P_{\max} , with birth sex ratio biases and constant fecundity (0.67) in the deterministic model. The time to minimum viable adult population (MVAP) is given when the P_{\max} value is exceeded by one individual annually, resulting in a sub-population decline. Persecution rates were increased from one individual annually for each age-class (with persecution rates for other age-classes at zero).

		Best-case scenario		Average-case scenario	
	Age-class	P_{\max}	Time to MVAP	P_{\max}	Time to MVAP
$b = 0.25$ (male-biased)	Cubs (0–1)	1	31	0	80
	Cubs (1–2)	1	23	0	37
	Sub-adults (2–3)	1	21	0	29
	Sub-adults (3–4)	1	18	0	25
	Adults (≥ 4)	1	11	0	23
$b = 0.50$ (equal ratio)	Cubs (0–1)	3	70	2	59
	Cubs (1–2)	3	23	2	20
	Sub-adults (2–3)	3	20	1	43
	Sub-adults (3–4)	2	23	1	22
	Adults (≥ 4)	2	9	1	14
$b = 0.75$ (female-biased)	Cubs (0–1)	6	28	4	59
	Cubs (1–2)	5	25	3	25
	Sub-adults (2–3)	5	20	3	19
	Sub-adults (3–4)	4	12	2	19
	Adults (≥ 4)	3	4	2	8

Table C.7. The maximum sustainable age-specific persecution rates, P_{\max} , with changes in fecundity (30% above and below the mean of 0.67) and sex ratio at parity ($b = 0.50$). The time to minimum viable adult population (MVAP) is given for when the P_{\max} value is exceeded by one individually annually, resulting in a population decline. Persecution rates were increased from one individual annually for each age-class, while keeping persecution rates for other age-classes at zero.

	Age-class	Best-case scenario		Average-case scenario	
		P_{\max}	Time to MVAP	P_{\max}	Time to MVAP
$f = 0.47$ (-30%)	Cubs (0–1)	2	29	1	43
	Cubs (1–2)	2	20	1	22
	Sub-adults (2–3)	2	19	1	19
	Sub-adults (3–4)	1	42	1	17
	Adults (≥ 4)	1	19	1	10
$f = 0.67$ (mean)	Cubs (0–1)	3	70	2	59
	Cubs (1–2)	3	23	2	20
	Sub-adults (2–3)	3	20	1	43
	Sub-adults (3–4)	2	23	1	22
	Adults (≥ 4)	2	9	1	14
$f = 0.87$ (+30%)	Cubs (0–1)	5	27	4	25
	Cubs (1–2)	4	28	3	20
	Sub-adults (2–3)	4	21	2	24
	Sub-adults (3–4)	3	18	2	15
	Adults (≥ 4)	2	20	2	7

Table C.8. The maximum sustainable age-specific persecution rates, P_{\max} , under extreme fecundity rates and birth sex ratio biases. These conditions represent the most pessimistic and optimistic scenarios for the lion sub-population.

	Age-class	Best-case scenario		Average-case scenario	
		P_{\max}	Time to MVAP	P_{\max}	Time to MVAP
$f = 0.47$ & $b = 0.25$	Cubs (0–1)	0	56	0	30
	Cubs (1–2)	0	41	0	23
	Sub-adults (2–3)	0	36	0	22
	Sub-adults (3–4)	0	32	0	21
	Adults (≥ 4)	0	29	0	16
$f = 0.87$ & $b = 0.75$	Cubs (0–1)	8	33	6	39
	Cubs (1–2)	7	24	4	39
	Sub-adults (2–3)	7	20	3	20
	Sub-adults (3–4)	5	12	3	15
	Adults (≥ 4)	3	9	2	13

Table C.9. Population resilience in the deterministic model to instantaneous, severe perturbations directed at the adult female age-class only, in the best- and average-case scenarios under various birth sex ratio biases. The return time (years) indicates the rate of which the sub-population returns to within 37% its initial displacement from equilibrium. Resilience was measured as the reciprocal of the return time; the closer the value to 1, the higher the resilience. Cases where adult numbers recovered within less than one year are indicated by (-).

	Persecution rate (%)	Best-case scenario		Average-case scenario	
		Return time (years)	Resilience (years ⁻¹)	Return time (years)	Resilience (years ⁻¹)
$b = 0.25$ (male-biased)	20	3	0.33	6	0.17
	30	4	0.25	9	0.11
	40	5	0.13	13	0.08
$b = 0.50$ (equal ratio)	20	-	-	2	0.50
	30	2	0.50	3	0.33
	40	2	0.50	4	0.25
$b = 0.75$ (female-biased)	20	-	-	-	-
	30	1	1	2	0.50
	40	1	1	2	0.50

Table C.10. Population resilience in the deterministic model to once off, severe perturbations directed at the adult female age-class only, in the best- and average-case scenarios and under variable fecundity rates. Cases where adult numbers recovered within less than one year are indicated by (-).

	Persecution rate (%)	Best-case scenario		Average-case scenario	
		Return time (years)	Resilience (years ⁻¹)	Return time (years)	Resilience (years ⁻¹)
$f = 0.47$ (-30%)	20	2	0.50	4	0.25
	30	3	0.33	6	0.17
	40	3	0.33	8	0.13
$f = 0.67$ (mean)	20	-	-	2	0.50
	30	2	0.50	3	0.33
	40	2	0.50	4	0.25
$f = 0.87$ (+30%)	20	-	-	2	0.50
	30	2	0.50	2	0.50
	40	2	0.50	3	0.33

Table C.11. The viability of the model sub-population subject to human-caused mortality, k_i , and environmental stochasticity, with changes in female fecundity ($f = 0.47$, 0.67 , and 0.87). The percentage, S , of simulation runs indicate the probability of the sub-population surviving above the MVAP for the duration of 50 years. Sensitivity to persecution increased with increasing age, with the adult age-class unable to sustain the loss of one adult annually (maximum probability being 44% with mean birth sex ratio and upper extreme fecundity rate).

		Age-class									
		Cubs (0–1)		Cubs (1–2)		Sub-adults (2–3)		Sub-adults (3–4)		Sub-adults (≥4)	
		k_i	S	Mean time to MVAP	S	Mean time to MVAP	S	Mean time to MVAP	S	Mean time to MVAP	S
$f = 0.47$ & $b = 0.50$	0	97%	35	97%	36	97%	35	96%	37	97%	37
	1	58%	36	25%	33	11%	29	6%	27	1%	18
	2	0%	27	0%	20	0%	16	0%	13	0%	8
	3	0%	19	0%	17	0%	14	0%	10	0%	5
	4	0%	19	0%	17	0%	14	0%	9	0%	4
	5	0%	19	0%	17	0%	14	0%	9	0%	3
$f = 0.67$ & $b = 0.50$	0	99%	34	100%	36	100%	35	100%	42	100%	38
	1	91%	33	82%	33	67%	32	57%	30	15%	24
	2	64%	35	15%	30	2%	22	0%	17	0%	9
	3	2%	28	0%	19	0%	14	0%	10	0%	5
	4	0%	20	0%	17	0%	14	0%	9	0%	4
	5	0%	19	0%	17	0%	14	0%	9	0%	3
$f = 0.87$ & $b = 0.50$	0	100%	22	100%	32	100%	44	100%	49	100%	49
	1	98%	32	95%	34	86%	30	83%	31	44%	25
	2	94%	35	71%	33	40%	29	18%	23	0%	12
	3	64%	35	10%	27	0%	18	0%	11	0%	6
	4	7%	29	0%	19	0%	14	0%	9	0%	4
	5	0%	21	0%	17	0%	14	0%	9	0%	3

Table C.12. The viability of the model sub-population subject to human-caused mortality, k_i , and environmental stochasticity, with changes in birth sex ratio ($b = 0.25, 0.50$, and 0.75). The percentage, S , of simulation runs indicate the probability of the population surviving above the MVAP for the duration of 50 years.

		Age-class									
		Cubs (0–1)		Cubs (1–2)		Sub-adults (2–3)		Sub-adults (3–4)		Sub-adults (≥4)	
		k_i	S	Mean time to MVAP	S	Mean time to MVAP	S	Mean time to MVAP	S	Mean time to MVAP	S
$f = 0.67$ & $b = 0.25$	0	84%	37	83%	38	85%	38	84%	36	83%	37
	1	3%	31	0%	25	0%	22	0%	19	0%	14
	2	0%	19	0%	18	0%	15	0%	13	0%	7
	3	0%	19	0%	17	0%	14	0%	10	0%	5
	4	0%	19	0%	17	0%	14	0%	9	0%	4
	5	0%	19	0%	17	0%	14	0%	9	0%	3
$f = 0.67$ & $b = 0.50$	0	99%	35	100%	42	99%	37	100%	32	100%	36
	1	92%	33	80%	34	68%	33	59%	31	17%	24
	2	62%	36	15%	30	2%	23	0%	17	0%	9
	3	2%	28	0%	19	0%	14	0%	10	0%	5
	4	0%	20	0%	17	0%	14	0%	9	0%	4
	5	0%	19	0%	17	0%	14	0%	9	0%	3
$f = 0.67$ & $b = 0.75$	0	100%	-	100%	-	100%	31	100%	-	100%	-
	1	99%	29	96%	34	93%	32	90%	28	58%	25
	2	98%	35	86%	33	65%	29	45%	25	2%	14
	3	90%	36	46%	31	8%	23	0%	13	0%	6
	4	51%	34	2%	24	0%	16	0%	9	0%	4
	5	6%	27	0%	18	0%	14	0%	9	0%	3

Table C.13. The viability of the model sub-population subject to human-caused mortality, k_i , environmental stochasticity and extreme rates of fecundity and birth sex ratio. A combination of the lower extreme rates of fecundity ($f = 0.47$) and birth sex ratio ($b = 0.25$), and upper extremes ($f = 0.87$, $b = 0.75$), represent the most pessimistic and optimistic scenarios respectively under the stochastic conditions. The percentage, S , of simulation runs indicate the probability of the sub-population surviving above the MVAP for the duration of 50 years. Even with the most optimistic fecundity and birth sex ratio rates, the maximum survival probability is 78 and 13% respectively when only one or two adults are persecuted annually.

		Age-class									
		Cubs (0–1)		Cubs (1–2)		Sub-adults (2–3)		Sub-adults (3–4)		Sub-adults (≥4)	
		k_i	S	Mean time to MVAP	S	Mean time to MVAP	S	Mean time to MVAP	S	Mean time to MVAP	S
$f = 0.47$ & $b = 0.25$	0	48%	36	46%	37	50%	37	47%	37	46%	36
	1	0%	23	0%	20	0%	18	0%	17	0%	12
	2	0%	19	0%	18	0%	15	0%	13	0%	7
	3	0%	19	0%	17	0%	14	0%	10	0%	5
	4	0%	19	0%	17	0%	14	0%	9	0%	4
	5	0%	19	0%	17	0%	14	0%	9	0%	3
$f = 0.87$ & $b = 0.75$	0	100%	-	100%	-	100%	-	100%	-	100%	-
	1	100%	29	99%	34	97%	25	96%	28	78%	25
	2	99%	34	96%	30	90%	26	78%	22	13%	16
	3	98%	36	88%	30	60%	26	30%	19	0%	8
	4	94%	34	61%	31	16%	23	1%	12	0%	4
	5	77%	34	13%	26	0%	17	0%	9	0%	3

